

COMMON LOON NESTING ECOLOGY IN NORTHWEST MONTANA

by

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ABSTRACT

Common Loons (*Gavia immer*) are found across the northern continental United States and in Canada and Alaska. The common loon is long lived, with delayed breeding maturity and low fecundity. Surveys indicate Montana's Common Loon population remains stable, but lakeshore development and watercraft recreation are increasing. While the effects of these changes are unclear, research investigating reproductive success over a gradient of habitat conditions, at multiple spatial scales is lacking. The objectives of this research were to investigate vital rates and the relationships between daily nest survival, chick survival and environmental covariates across multiple spatial scales. I monitored seventy-nine Common Loon nesting attempts and the fates of sixty-five Common Loon chicks during two field seasons in Montana. The strongest predictor of nest survival was the type of breeding territory occupied by loons. Loon nests on small lakes (<60 acres) showed the highest nest survival, followed by nests established on large lakes (>60 acres) occupied by a single breeding pair. The lowest nest survival occurred on large lakes (>60 acres) occupied by two or more breeding pairs. I found effects of landscape and lake scale covariates on chick survival, where chick survival was positively related to the number of foraging lakes, and number of adjacent pairs, within a 10-km radius of the nest. I observed a negative association between recreation activity and chick survival. Management actions designed to affect nest survival must vary depending on the type of nesting territory targeted. Management priorities for all territory types should focus on maintaining and restoring shoreline and island nesting habitat, and modifying watercraft recreation during the nesting period. Because small nesting lakes were the most productive, MLT areas should receive the highest attention. Land use planners involved with MLT lakes should consider minimizing watercraft disturbance on adjacent lakes to maintain, or improve, adult foraging habitats. Finally, efforts to increase chick survival need to focus on minimizing the negative effects of human recreation, especially during the first week post-hatching. Temporary "no wake" restrictions, or using floating signs to eliminate watercraft use in historical chick nursery areas, may increase chick survival.

INTRODUCTION

Common loons (*Gavia immer*) are distributed across the northern continental United States and into Canada and Alaska. Loons are one of the largest birds in the north temperate region, weighing 3.6-5.5 kg (Evers 2002). Loons breed on freshwater lakes then migrate to the Pacific or Atlantic Coast during winter. The common loon is long lived (25-30 yrs.) and exhibits delayed breeding maturity and relatively low fecundity (Evers 2002). Diving specialists, their relatively large densely calcified leg bones attach at the anterior caudal region and are entirely enclosed by caudal patagia (McIntyre, 1988). Loons have been captured in fishing nets at depths of 60.96-m in the Great Lakes region (Olson 1951). The anterior position of the legs makes the loon an efficient swimmer but severely limits the ability to walk on land. As a result, loons come ashore primarily to nest and breed, with nests typically located within 1-m of water (Vermeer 1973).

Information concerning loon population vital rates and habitat use comes primarily from studies conducted in New England and the Upper Great Lakes (Evers 2004). In that region, estimates of chick survival, i.e., from hatch to 4-6 weeks of age, ranged from 0.62-0.93 (Clay and Clay 1997, Croskery 1991, Kelly 1992), while juvenile survival (i.e., 1-3 yrs.) ranged between 0.17-0.41 (Paruk et. al, 2000, Evers 2004). The average age of first breeding was seven, and adult (i.e., >3 yr. old) annual survival rates ranged from 0.91-0.97. Juvenile loons that survived to breed typically established territories within 16-km of their hatch site (Evers 2002). Most mortality for loons has been associated with the non-breeding season, during juvenile migration, or during the

first 2.5 years when juveniles remain on the coasts. Little is known about common loon migration routes and staging areas, or how stop-over habitats might affect juvenile and adult survival.

Bird populations located along the periphery of their range often fluctuate more than within core areas because population fragmentation and local extinctions can reach high levels near population edges (Mehlman 1997). Montana's common loon population exists along the southern fringe of the species range in the western U.S., thus a primary regional management goal is to prevent population fragmentation and reduction of suitable lake habitats (Bissell 2005). Because identifying threats to loon nesting and foraging habitat is vital for loon persistence, my investigation of factors influencing reproductive success of Montana's loon population is highly warranted.

The research presented in this thesis was designed to investigate the nesting ecology of Common Loons in northwest Montana. This research is the first segment of a two part Montana Fish, Wildlife and Parks Loon Ecology Project, funded by a State Wildlife Grant (SWG). It is my hope that results from this research will be used to inform conservation strategies and supplement information in the current Montana Common Loon Management Plan (Skaar 1990). Observational field surveys were selected as my primary method of study because they were cost effective and efficient for monitoring a highly visible and vocal species such as loons. The objectives of this study were to: (1) evaluate the effects of physical habitat characteristics and human disturbance (both recreation and development) on loon nest survival at multiple spatial scales, (2) evaluate the effects of physical habitat characteristics and human disturbance

on loon chick survival at multiple spatial scales, and (3) use an information theoretic approach, coupled with AIC model evaluation, to test a priori hypotheses concerning the relationships between response variables and habitat based explanatory variables. My thesis includes both nest and chick survival chapters that are intended for publication in peer-reviewed journals following format adjustments. I have combined all references in the thesis within a comprehensive Literature Cited section.

Study Area

This research was conducted within northwest Montana between 47.00⁰ and 49.00⁰ N latitude and 115.20⁰ and 113.40⁰ W longitude, encompassing portions of Flathead, Lincoln, and Lake Counties within Montana Fish Wildlife and Park's (MFWP) Region One. MFWP annual loon surveys indicate the loon population in the region includes 150-200 adults that produce between 30-50 chicks per year (Bissell 2005). Breeding pairs have been located primarily north of Missoula and west of the Continental Divide, with few records of loons breeding east of the Divide. During my research, field work was conducted in two primary areas: along U.S. Highway 93 between Kalispell and Eureka; and along U.S. Highway 2 between Kalispell and Libby (Figure 1).

Within the two study areas, upland vegetation was dominated by mixed conifer forests, whereas bottomland and river valleys were dominated by thick stands of willow (Salix. spp.). Timber harvest, livestock grazing, and recreation were the primary human land uses in the study area. In addition, some crop production occurred in river valleys and adjacent uplands. Vegetation coverage was strongly influenced by cold winters with heavy snowfall, cool wet springs, and warm summer climate. Temperatures varied from

-37 °C to over 37 °C with average daily temperatures in January and July of -5.89 °C and 17.5 °C respectively. Average annual precipitation was 43.71-cm with most precipitation occurring during May and June (<http://www.ncdc.noaa.gov/oa/climate>). Ice out typically occurred on area lakes in early April during my study.

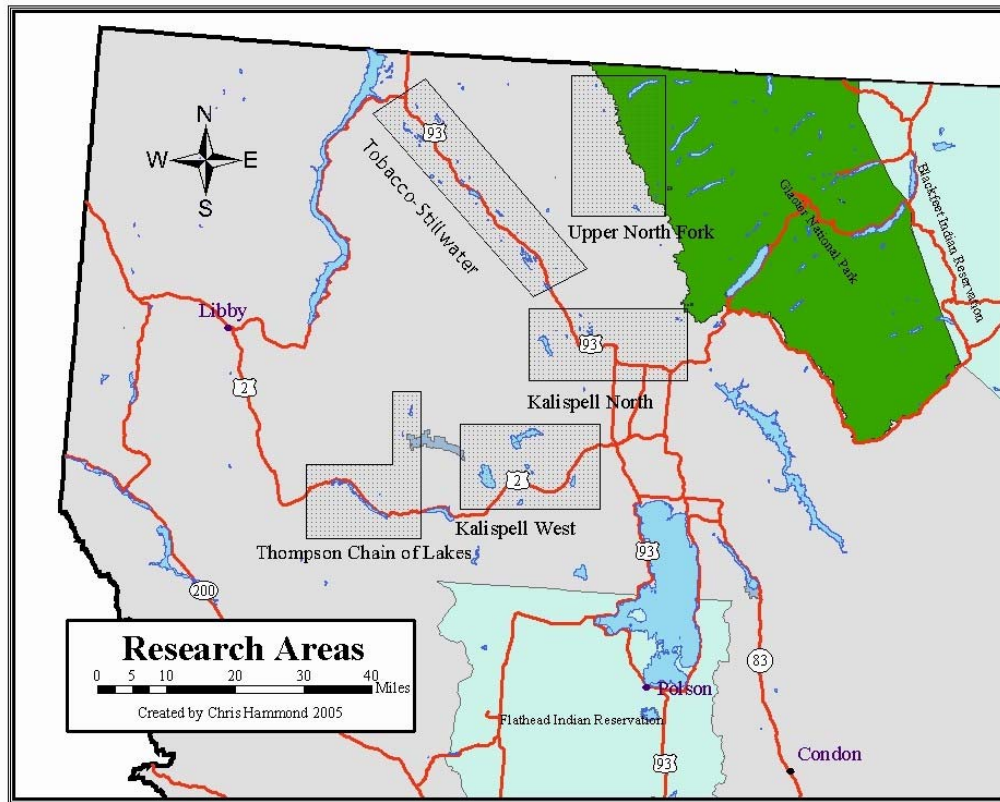


Figure 1. Location of study sites in the northwest Montana, USA, 2004-2005. The stippled and grey-shaded polygons depict lake clusters where I systematically searched for nesting loons, and monitored chicks post-hatch.

FACTORS AFFECTING NEST SURVIVAL OF COMMON LOONS IN NORTHWEST MONTANA

Introduction

Nest survival estimates are a key component of reproductive output often targeted for management of avian species. Variation in nest survival is thought to be a sensitive indicator of environmental effects (Armstrong et al. 2001), and yet the relationship among different environments, disturbance levels, and their connections to loon nest survival are unclear. Current MFWP -management strategies targeting loon reproductive vital rates primarily involve public education about responsible watercraft use in loon nesting habitat and organized surveys to monitor abundance of adults and young (Bissell, 2005). However, limited data are available about how loon reproductive success is affected by habitat setting and human disturbance, especially at multiple spatial scales. Given the lack of relevant information on affects of physical habitat characteristics, human development and thresholds of lake suitability, further research investigating nesting biology of loons in Montana is needed.

While the effects of lake-side human developments on loons in Montana may be negative, the extent of the impact to loon nesting success remains uncertain. Sutcliffe (1980) observed 205 nesting attempts in New Hampshire and suggested that human disturbance was a significant threat to nest success. Loons nested more frequently on lakes with little or no human disturbance and, further, hatching success was shown to decline as the number of cottages within 150-m of nest sites increased (Heimberger et al. 1983). In Northeastern Minnesota, an area composed of numerous small to medium size

lakes, reproductive success was highest on lakes where no motors were allowed on watercraft versus lakes without motor restrictions (Titus et al. 1981).

Lake-based recreation and lake-side home development have increased dramatically on lakes in northwest Montana during the last decade (www.flatheadbasincommission.org). Human lakeshore development, water based recreation, and other unknown habitat factors could negatively affect loon nest survival. Increasing habitat fragmentation may represent a key threat because nesting lakes are already widely scattered. Because loons are slow to pioneer or re-colonize new habitats, if loons fail to produce chicks for consecutive years, the population could experience local extinctions. Increasing isolation and small population size can further reduce gene flow among subpopulations and loss of genetic diversity (Pannell and Charlesworth 2000).

Although loon survival and recruitment rates have been documented through mark/re-sight studies in the Eastern United States (Evers 2004), information on population vital rates and other characteristics, such as territory fidelity, are unknown in Montana. Because both breeding and winter habitats vary widely in North America, applying east-based vital rate and habitat knowledge to western loons may not be appropriate. Given the lack of local studies on loon population and habitat characteristics, the objectives of this study were to evaluate the relationships between daily nest survival rates and relevant environmental covariates across multiple spatial scales, including investigations of nest site characteristics, individual lakes, and clusters of lakes across the landscape. In addition, my objective was to use an information

theoretic approach, coupled with AIC model evaluation, to test a priori hypotheses concerning the relationships between response variables and habitat based explanatory variables.

This research focused on three spatial scales to investigate associations among nest survival and habitat. At the nest scale of study, the primary research questions included, (1) what is the relationship among nest location, nest cover and daily nest survival rate?, and (2) what is the association between human use and development, nest location and cover, and daily nest survival (DSR)? I hypothesized that, (1) loons nesting on islands and platforms will show higher DSR than loons nesting on mainland nests; (2) floating platform nests will not be affected by water level changes to the extent that mainland nests are affected; (3) nests that possess any of three cover types [sedge/grass, cattail/reed, or shrub] will have higher daily survival rates than nests with no cover; (4) there will not be a significant difference in DSR among cover types; and (5) nests with deep water within 1-m from the nest will have higher DSR than nests with shallow water near the nest. My hypotheses concerning effects of covariates on nest survival were rooted in the following assumptions: (1) island and platform nests will experience lower rates of predation by mammalian shoreline predators, (2) nests on artificial platforms float at the current water level, thus eliminate the possibility of flooding or stranding, (3) deep water near the nest allows a loon to enter and leave the nest under water without drawing attention of predators, (4) nests with greater amounts of habitat cover will have relatively higher DSR because cover may ameliorate nest disturbance, e.g., nest cover could allow incubating loons to remain hidden on nests during watercraft disturbances.

At the lake scale of study, I identified two research questions, first, how do physical habitat characteristics, including measures of human use (e.g., development indices and recreation level), affect the magnitude of loon DSR among different lake settings? Second, how does human-use and development interact with physical habitat variables to influence variance in DSR? I hypothesized that (1) lakes with higher measures of human disturbance will experience significantly lower DSR than lakes with moderate or no human disturbance, (2) lakes with the lowest level of human disturbance would show the highest DSR, (3) DSR would be strongly influenced by physical habitat characteristics including water fluctuation, lake surface area, perimeter, and shoreline development index, and (4), if lakeshore complexity was related to predator nest searching, then more complex shorelines would provide loons a broad range of nesting opportunities resulting in increased predator search time per nest and higher DSR.

Implicit in my induction concerning lake-scale effects were four assumptions: (1) as the amount of human-developed shoreline increases, nest site availability decreases, and overall nest site quality declines, e.g. loons might be displaced toward nest areas with lower nest cover or prey availability; (2) recreation activities, e.g., boating or canoeing, have been shown to flush incubating loons from nests (Kelly 1992), thus recreation pressure will cause loons to spend more time off nests, and eggs will be more vulnerable to cooling or predation; (3) a decrease in shoreline cover by live trees, shrubs and woody structure caused by increased human development (Christensen et al. 1996) increases nest vulnerability to predation by concentrating nest predators in smaller shoreline habitat patches; and (4), predator assemblages will change in response to

human activity or development, e.g., crows and bald eagles may be drawn to lakes in response to human activity (Verbeek 1982).

At the landscape scale, my research questions included: (1) does the abundance of adjacent lakes in the vicinity of the nest lake affect nest DSR, e.g., positively via increased forage opportunities or negatively via increased territorial conflict with neighbors? (2) How do breeding territory (Evers 2001) and habitat variables interact with the number of feeding lakes and breeding pairs within a 10-km radius? I hypothesized that (1) large lakes with one nesting pair (whole lake territories) will have the highest DSR followed by large lakes with two or more nesting pairs (partial lake territories), while small lakes with one nesting pair (multi-lake territories, <60 acres) will exhibit the lowest nest DSR, (2) DSR will be positively related to the number of feeding lakes within a 10-km radius of the nesting lake (FL10), and (3), DSR will be negatively related to the number of breeding pairs within a 10-km radius of the nest lake.

My hypotheses concerning landscape effects on DSR were based on five assumptions: (1) whole lake territories provide sufficient forage resources for adults to minimize flights to nearby lakes, thus increasing nest vigilance by both adults, (2) the existence of potential feeding lakes near the nesting lake provides breeding adults greater foraging opportunities, (3) multiple adjacent feeding lakes may allow adults to forage more efficiently if factors such as human recreation increase significantly on the nesting lake, (4) neighboring pairs located near the focal nest may increase the occurrence of territorial conflicts, keeping incubating adults off nests for extended periods of time, increasing egg vulnerability to cooling or predation, and (5), as loon densities increase,

and more lakes are occupied or divided among greater numbers of loon territories, site fidelity, DSR, and overall reproductive success will decline (Evers 2002).

METHODS

Data Collection

Numerous lakes in NW Montana historically hosted breeding loons or showed evidence of loon presence (MFWP, Loon Day Survey, unpubli. Records). Forty-seven lakes were selected for nest monitoring and research investigating population vital rates and covariates. All lakes in the sample were visited at least twice each spring to search for signs of nesting loons, however three lakes (Lost, Murray, Skyles) were censored from the sample because loons were not observed during project initiation in 2004. To locate loon nests, observers monitored loon behavior on each of the selected lakes using 20X-60X spotting scopes. Once a suspected nest area was pinpointed, systematic searches were conducted along the shoreline to locate the nest. Nest searches began in May each year, and monitoring was conducted through June, with all “historic” nesting lakes (i.e., lakes known to have previous nesting) monitored every 1-7 days to locate nests and record nest status. To increase detection rate of nests and minimize missing failed nest attempts, the interval between nest visits was decreased during the initial search period when loons were exhibiting clear signs of breeding (e.g., searching along the shoreline, nest building).

Established nests were visited every 4-7 days throughout the incubation period to assess egg and nestling status. During the nest visits, most observations were conducted with spotting scopes from 50-500 m away to minimize observer disturbance. During each observation period, the status of the nest (incubating, abandoned or hatched),

adult behavior, water level, weather, and watercraft use and recreation on the nesting lake were recorded on field data forms. A nest was labeled “abandoned” when no adults were observed incubating during two consecutive visits. Because incubating loons have a propensity for nest abandonment if disturbed (Sutcliffe 1980, Kelly 1992), nests were not approached closely (i.e., within 50-m) until after hatching, or once abandonment was suspected.

Nest habitat covariates were summarized at three spatial scales to represent covariates that could influence nest survival: micro-site (i.e., ≤ 5 -m from the nest), nesting lake, and landscape. After confirmed fledging or nest abandonment, the site was visited to measure micro-site habitat covariates, including: nest location (island, mainland associated, or platform), nest cover (sedge/grass, cattail/reed, shrub, none), and water depth 1-m from the nest. At the lake spatial scale, the following data were collected: surface area, mean depth, and shoreline development index (SDI), a measure of lake edge complexity, calculated by:

$SDI = L/2\sqrt{\pi A}$, where L is the length of the shoreline and A is the surface area of the lake. SDI is a comparative figure relating the shoreline length to the circumference of a circle that has the same area as the lake. The smallest possible SDI value = 1.0 would be produced by a perfect circle, thus shoreline irregularities (e.g., coves, inlets) increase SDI (Cole 1994).

To create a prey resource covariate for subsequent modeling, the presence and abundance of Yellow Perch (*Perca flavescens*) and Northern Pike were measured at each lake, using MFWP field estimates of fish abundance (MFWP, unpubl. Data). In

addition, angling pressure information was obtained for each lake (MFWP 2001, 2003), and human disturbance was measured using a technique developed by Vermeer (1973). Angler pressure reports were compiled biannually for the summer and winter fishing seasons, with the 2001 and 2003 pressure reports available as the most current data for my analyses. I averaged angler trips during the summer 2001 and 2003 angling seasons to obtain mean number of angler trips (MAT) for each lake. Angler trip numbers from 2001 and 2003 were similar for individual lakes between years and were assumed to represent a reasonable measure of angler use during the 2004 and 2005 study seasons.

To calculate Vermeer disturbance ratios, ten disturbance units were assigned to each government campsite and resort, where 5 points were assigned for each un-maintained public access site, and 1 disturbance point was assigned for each house and summer home bordering a lake. The total number of disturbance units calculated for each lake was divided by the lake surface area to obtain the disturbance ratio in relation to surface area (VDRSA). The number of disturbance points was divided by lake perimeter to calculate VDRPER. For example, a lake with 3 homes (3 pts.), 1 public boat launch (10 pts.), and 2 un-maintained public access sites (10 pts.) with 250 acres of surface water and a 4300-m perimeter would have the following disturbance index:

$$\text{VDR(SA)} = (3 + 10 + 10) / 250 = 0.0920,$$

$$\text{VDR(PER)} = (3 + 10 + 10) / 4300 = 0.0053$$

Three landscape scale habitat variables were measured for each lake: (1) the number of breeding pairs located within a 10-km radius from the nest (BP10); (2) the number of feeding lakes larger than 8-ha and not occupied by an established territorial loon pair located within 10-km radius from the nest (FL10); and (3) territory type: multiple-(MLT), whole-(WLT), and partial-lake territories (PLT) (Evers 2001).

Modeling Nest Survival

Traditionally, estimates of nest survival are assessed using the Mayfield Estimator (Mayfield 1961), which yields a constant daily survival rate (i.e., DSR) for all nests in a sample and minimizes bias associated with apparent nest success (Rotella et al. 2004). If a nest fails in the period between nest visits, the failure date is assigned to the midpoint of the interval between nest visits (Mayfield 1961). DSR was defined as the probability that a nest would survive a single day, and nest survival as the probability that a nest would be successful (Dinsmore et al. 2002). A successful nest was defined as one that produced at least one chick.

The nest survival module of Program MARK operates under 5 basic assumptions: (1) nests can be correctly aged when they are first found; (2) nest fates are correctly determined; (3) nest discovery and subsequent nest checks do not influence survival; (4) nest fates are independent; (5) daily nest survival rates are homogeneous. The nest survival model requires the following information for each nest: (1) the day the nest was found; (2) the last day the nest was checked alive; (3) the last day the nest was

checked; (4) the fate of the nest (0=successful, 1= destroyed or unsuccessful); (5) the number of nests with this encounter history (Dinsmore et al. 2002).

Program MARK (White and Burnham 1999) was also used to evaluate variation in nest survival as a function of the habitat covariates at multiple spatial scales. Because MARK is not restricted to constant DSR during incubation, I evaluated continuous variables, temporal trends and non-interacting effects (Jehle et al. 2004, Rotella et al. 2004). Although investigators have often used sequential null hypothesis tests and step-wise procedures to screen habitat covariates for significant effects, these procedures have been criticized for unsound inference (Chatfield 1995, MacNally 2000, Royall 1997, Burnham and Anderson 2002). Akaike's information criterion (AIC) provides an alternative to traditional analyses to evaluate habitat associations. An information criterion estimates the amount of information lost when using a particular model to approximate reality compared with other models; better models lose less information (Burnham and Anderson 2002). Because results depend on the entire set of candidate models, models should be identified before data analysis.

In exploring species-habitat associations, my goal was to use AIC methods to quantify the relative importance of habitat variables, provide evidence for association to assess hypotheses, and identify combinations of variables best used for prediction. The AIC model weights were examined to evaluate evidence in support of a particular model compared to other models in a candidate list. Model averaging was used to derive slope estimates from among the best approximating models. The fate of an individual nest was assumed to be independent of other nest fates.

The modeling approach for loons incorporated existing data combined with data collected during field investigations (Table 1). Literature about loon nesting habitat, as well as studies that documented effects of human disturbance on nest success inductively influenced the hypothesized habitat-DSR associations (Table 2). The stated hypotheses led to the construction of several candidate lists of a priori models (Table 3). To construct each model set, I started with single predictor models and then added models containing combinations of covariates I believed were biologically relevant to DSR. Finally, I added models to each candidate set that represented potential interactions that might influence nest survival. Candidate models were divided among hypothesized suites, including: (1) models associated with the effects of human disturbance on DSR; (2) habitat structure (3) models exploring predation effects, and (4) combinations of the first three suites that might represent the best approximating model (Burnham and Anderson 2002)(Table 3). Selection of the best approximating model for DSR was evaluated using the nest survival module in Program MARK (White and Burnham 1999). Daily survival rates were estimated using coefficients derived from the best approximating model in the DSR all Models Suite. Sets of candidate models were run with the parameter index matrices set for constant daily survival following the maximum likelihood version of the Mayfield Model (Cooch and White 2005).

Table 1. Nest-site, lake and landscape scale variables measured during field research 2004, 2005 with abbreviations and definitions.

Covariate	Definition
BP10	Number of breeding pairs within 10 km radius from nesting lake
FL10	Number of feeding lakes (lakes without breeding pairs) within 10 km radius from the nest
LSA	Lake surface area
MAT	Mean angler trips
MLD	Mean lake depth
NCOV	Nest cover (sedge/grass, cattail, shrub, none)
NL	Nest location (island, mainland, platform)
PERIM	Shoreline perimeter
SDI	Shoreline development index (measure of shoreline complexity)
TER	Territory type (multi-lake, whole lake, partial-lake)
VDR(PER)	Vermeer disturbance ratio (measure of human development and recreation use of the lake in relation to lake perimeter)
VDR(SA)	Vermeer disturbance ratio (measure of human development and recreation use of the lake in relation to lake surface area)
WD1M	Water depth one meter from nest
WTRFL	Water fluctuation during incubation period
YR	Year

Table 2. Hypothesized effects of covariates on nest DSR.

Spatial Scale	Covariate	Covariate sub-type	Effect (slope)
<u>Micro-site</u>	WD1M		$\beta > 0$
	NL	Mainland	$\beta < 0$
		Island	$\beta > 0$
		Platform	$\beta > 0$
	NCOV	Sedge/Grass	$\beta > 0$
		Cattail/Reed	$\beta > 0$
		Shrub	$\beta > 0$
		None	$\beta < 0$
<u>Lake</u>	WTRFL		$\beta < 0$
	LSA		$\beta > 0$
	PERIM		$\beta > 0$
	SDI		$\beta > 0$
	MLD		$\beta < 0$
	VDR(SA)		$\beta < 0$
	VDR(PER)		$\beta < 0$
	MAT		$\beta < 0$
<u>Landscape</u>	BP10		$\beta < 0$
	FL10		$\beta > 0$

Table 2 Cont. Hypothesized effects of covariates on nest DSR.

Spatial Scale	Covariate	Covariate sub-type	Effect (slope)
	TER	Whole Lake	$\beta > 0$
		Partial Lake	$\beta < 0$
		Multiple Lake	$\beta < 0$

Table 3. A priori Nest Survival Model List.

Model	Model structure
Disturbance suite	
{DSR(MAT)}	DSR=B0+B1(MAT)
{DSR(VDRPER)}	DSR=B0+B1(VDRPER)
{DSR(VDRSA)}	DSR=B0+B1(VDRSA)
{DSR(WD1M+ MAT)}	DSR=B0+B1(WD1M)+B2(MAT)
{DSR(LSA + MAT)}	DSR=B0+B1(LSA)+B2(MAT)
{DSR(SDI + MAT)}	DSR=B0+B1(SDI)+B2(MAT)
{DSR(SDI + MAT + SDI*MAT)}	DSR=B0+B1(SDI)+B2(MAT)+B3(SDI*MAT)
{DSR(LSA + MAT + LSA*MAT)}	DSR=B0+B1(LSA)+B2(MAT)+B3(LSA*MAT)
{DSR(VDRPER+ NCOV)}	DSR=B0+B1(VDRPER)+B2(SEDGRASS) +B3(CATTREED)+B4(SHRUB)
{DSR(VDRSA + NCOV)}	DSR=B0+B1(VDRSA)+B2(SEDGRASS) +B3(CATTREED)+B4(SHRUB)
{DSR(MAT + SDI + NCOV)}	DSR=B0+B1(MAT)+B2(SDI)+B3(SEDGRASS) +B4(CATTREED)+B5(SHRUB)
{DSR(VDRSA + NL + NCOV)}	DSR=B0+B1(VDRSA)+B2(SHORE)+B3(ISLAND) +B4(SEDGRASS)+B5(CATTREED)+B6(SHRUB)
{DSR(MAT+ NCOV + MAT*NCOV)}	DSR=B0+B1(MAT)+B2(SEDGRASS) +B3(CATTREED)+B4(SHRUB)+B5(MAT*SEDGRASS) +B6(MAT*CATTREED)+B7(MAT*SHRUB)
{DSR(VDRPER + NCOV + VDRPER*NCOV)}	DSR=B0+B1(VDRPER)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)+B5(VDRPER*SEDGRASS) +B6(VDRPER*CATTREED)+B7(VDRPER*SHRUB)
{DSR(VDRSA + NCOV + VDRSA*NCOV)}	DSR=B0+B1(VDRSA)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)+B5(VDRSA*SEDGRASS) +B6(VDRSA*CATTREED)+B7(VDRSA*SHRUB)

Table 3 cont. A priori Nest Survival Model List.

Model	Model structure
{DSR(VDRSA + NL + NCOV + YEAR)}	DSR=B0+B1(VDRSA)+B2(SHORE)+B3(ISLAND) +B4(SEDGRASS)+B5(CATTREED)+B6SHRUB +B7(YEAR)
Habitat suite	
{DSR(PERIM)}	DSR=B0+B1(PERIM)
{DSR(LSA)}	DSR=B0+B1(LSA)
{DSR(WTRFL)}	DSR=B0+B1(WTRFL)
{DSR(SDI)}	DSR=B0+B1(SDI)
{DSR(BP10)}	DSR=B0+B1(BP10)
{DSR(MLD)}	DSR=B0+B1(MLD)
{DSR(FL10)}	DSR=B0+B1(FL10)
{DSR(TER)}	DSR=B0+B1(MLT)+B2(WLT)
{DSR(SDI + PERIM)}	DSR=B0+B1(SDI)+B2(PERIM)
{DSR(TER + BP10)}	DSR=B0+B1(MLT)+B2(WLT)+B3(BP10)
{DSR(TER + FL10)}	DSR=B0+B1(MLT)+B2(WLT)+B3(FL10)
{DSR(WD1M + NL)}	DSR=B0+B1(WD1M)+B2(SHORE)+B3(ISLAND)
{DSR(LSA + MLD + SDI)}	DSR=B0+B1(LSA)+B2(MLD)+B3(SDI)
{DSR(WTRFL + NL)}	DSR=B0+B1(WTRFL)+B2(SHORE)+B3(ISLAND)
{DSR(TER + FL10 + TER*FL10)}	DSR=B0+B1(MLT)+B2(WLT)+B3(FL10) +B4(MLT*FL10)+B5(WLT*FL10)
{DSR(TER + BP10 + TER*BP10)}	DSR=B0+B1(MLT)+B2(WLT)+B3(BP10) +B4(MLT*BP10)+B5(WLT*BP10)
{DSR(WTRFL + NL + WTRFL*NL)}	DSR=B0+B1(WTRFL)+B2(SHORE)+B3(ISLAND) +B4(WTRFL*SHORE)+B5(WTRFL*ISLAND)
{DSR(WD1M + NL + NCOV)}	DSR=B0+B1(WD1M)+B2(SHORE)+B3(ISLAND) +B4(SEDGRASS)+B5(CATTREED)+B6(SHRUB)
Predation suite	
{DSR(PERIM)}	DSR=B0+B1(PERIM)
{DSR(YEAR)}	DSR=B0+B1(YEAR)
{DSR(SDI)}	DSR=B0+B1(SDI)

Table 3 cont. A priori Nest Survival Model List.

Model	Model structure
{DSR(NL)}	DSR=B0+B1(SHORE)+B2(ISLAND)
{DSR(NL + PERIM)}	DSR=B0+B1(SHORE)+B2(ISLAND)+B3(PERIM)
{DSR(NCOV)}	DSR=B0+B1(SEDGRASS)+B2(CATTREED) +B3(SHRUB)
{DSR(SDI + NL)}	DSR=B0+B1(SDI)+B2(SHORE)+B3(ISLAND)
{DSR(NL + PERIM + NL*PERIM)}	DSR=B0+B1(SHORE)+B2(ISLAND)+B3(PERIM) +B4(SHORE*PERIM)+B5(ISLAND*PERIM)
{DSR(SDI + NL + SDI*NL)}	DSR=B0+B1(SDI)+B2(SHORE)+B3(ISLAND) +B4(SDI*SHORE)+B5(SDI*ISLAND)
{DSR(NL + NCOV)}	DSR=B0+B1(SHORE)+B2(ISLAND)+B3(SEDGRASS) +B4(CATTREED)+B5(SHRUB)
{DSR(NL + NCOV + YEAR)}	DSR=B0+B1(SHORE)+B2(ISLAND)+B3(SEDGRASS) +B4(CATTREED)+B5(SHRUB) +B6(YEAR)
{DSR(NL + NCOV + NL*NCOV)}	DSR=B0+B1(SHORE)+B2(ISLAND)+B3(SEDGRASS) +B4(CATTREED)+B5(SHRUB) +B6(SHORE*SEDGRASS)+B7(SHORE*CATTREED) +B8(SHORE*SHRUB)+B9(ISLAND*SEDGRASS) +B10(ISLAND*CATTREED)+B11(ISLAND*SHRUB)
<hr/> Predation/habitat/disturbance suite <hr/>	
{DSR(VDRSA + TER)}	DSR=B0+B1(VDRSA)+B2(MLT)+B3(WLT)
{DSR(VDRPER + TER)}	DSR=B0+B1(VDRPER)+B2(MLT)+B3(WLT)
{DSR(MAT + TER)}	DSR=B0+B1(MAT)+B2(MLT)+B3(WLT)
{DSR(MAT + LSA + WD1M)}	DSR=B0+B1(MAT)+B2(LSA)+B3(WD1M)
{DSR(VDRPER + NCOV)}	DSR=B0+B1(VDRPER)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)
{DSR(MAT + NCOV)}	DSR=B0+B1(MAT)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)
{DSR(VDRSA + NCOV)}	DSR=B0+B1(VDRSA)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)
{DSR(MAT + TER + MAT*TER)}	DSR=B0+B1(MAT)+B2(MLT)+B3(WLT)+B4(MAT*MLT) +B5(MAT*WLT)
{DSR(VDRSA + TER + VDRSA*TER)}	DSR=B0+B1(VDRSA)+B2(MLT)+B3(WLT) +B4(VDRSA*MLT)+B5(VDRSA*WLT)
{DSR(VDRPER + TER + VDRPER*TER)}	DSR=B0+B1(VDRPER)+B2(MLT)+B3(WLT) +B4(VDRPER*MLT)+B5(VDRPER*WLT)
{DSR(VDRPER + NCOV + WD1M)}	DSR=B0+B1(VDRPER)+B2(SEDGRASS) +B3(CATTREED)+B4(SHRUB)+B5(WD1M)
{DSR(MAT + NCOV + LSA)}	DSR=B0+B1(MAT)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)+B5(LSA)
{DSR(VDRSA + NCOV + WD1M)}	DSR=B0+B1(VDRSA)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)+B5(WD1M)

Table 3 cont. A priori Nest Survival Model List.

Model	Model structure
{DSR(MAT + NCOV + NL)}	DSR=B0+B1(MAT)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)+B5(SHORE) +B6(ISLAND)
{DSR(NCOV + NL + WD1M)}	DSR=B0+B1(SEDGRASS)+B2(CATTREED)+B3(SHRUB) +B4(SHORE)+B5(ISLAND) +B6(WD1M)
{DSR(MAT + NCOV + MAT*NCOV)}	DSR=B0+B1(MAT)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)+B5(MAT*SEDGRASS) +B6(MAT*CATTREED)+B7(MAT*SHRUB)
{DSR(VDRPER + NCOV + VDRPER*NCOV)}	DSR=B0+B1(VDRPER)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)+B5(VDRPER*SEDGRASS) +B6(VDRPER*CATTREED)+B7(VDRPER*SHRUB)
{DSR(VDRSA + NCOV + VDRSA*NCOV)}	DSR=B0+B1(VDRSA)+B2(SEDGRASS)+B3(CATTREED) +B4(SHRUB)+B5(VDRSA*SEDGRASS) +B6(MAT*CATTREED)+B7(VDRSA*SHRUB)

In addition to evaluating a priori candidate models, exploratory analysis using stepwise procedures was conducted to examine how multi-scaled variables might influence estimates of loon nest DSR. I used a three step procedure to construct exploratory models. First, I examined the most highly supported a priori models and determined common covariates among the most supported models and their effects on DSR. I limited exploratory models to contain only covariates in the most highly supported models. Model structure allowed me to explore aspects of territoriality that might influence DSR, e.g, shoreline configuration, and explore interactions between territory type and the number of potential foraging lakes and breeding pairs within a 10 km radius of the nest (Table 4). Exploratory models were combined with a priori models within a final candidate set and evaluated for an overall comparison of effects.

Finally, because of the structure of the territory type covariate (Evers 2004), territory type could be correlated with other covariates, thus multi-collinearity could cause mis-interpretation of the significance of territory in my models. To increase my understanding of aspects of “territory type” that played a large role in daily nest survival,

I performed a separate non-model based exploratory analysis using underlying means and SE's summarized from continuous covariates when separated by territory type. This allowed me to examine how covariates that were not necessarily highly supported in the model suites changed among territory types. Essentially, this technique allowed me to explore aspects of different territory types that may have been overlooked in modeling results due to the overwhelming support of the territory covariate.

Table 4. DSR Exploratory Model Suite

Exploratory suite	
Model	Model Structure
{DSR(BPLAKE)}	DSR=B0+B1(BPLAKE)
{DSR(TER + PERIM)}	DSR=B0+B1(MLT)+B2(WLT)+B3(PERIM)
{DSR(TER + SDI)}	DSR=B0+B1(MLT)+B2(WLT)+B3(SDI)
{DSR(TER + LSA)}	DSR=B0+B1(MLT)+B2(WLT)+B3(LSA)
{DSR(TER + PERIM + TER*PERIM)}	DSR=B0+B1(MLT)+B2(WLT)+B3(PERIM) +B4(MLT*PERIM)+B5(WLT*PERIM)
{DSR(TER + SDI + TER*SDI)}	DSR=B0+B1(MLT)+B2(WLT)+B3(SDI) +B4(MLT*SDI)+B5(WLT*SDI)
{DSR(TER + FL10 + BP10+ FL10*BP10)}	DSR=B0+B1(MLT)+B2(WLT)+B3(FL10) +B4(BP10)+B5(FL10*BP10)
{DSR(TER + LSA + TER*LSA)}	DSR=B0+B1(MLT)+B2(WLT)+B3(LSA) +B4(MLT*LSA)+B5(WLT*LSA)

RESULTS

Common loon nests were observed on 27 unique lakes during the 2004 field season and 27 lakes during 2005. The number of lakes with nests remained constant between years and nearly all lakes with confirmed nesting during the 2004 season also had loons nesting during the 2005 nesting season. Overall, seventy-nine nesting attempts, including re-nests were monitored during the 2004 and 2005 breeding seasons. Thirty-eight nesting attempts were monitored on 27 lakes in 2004 and 41 nesting attempts were observed and monitored on 27 lakes in 2005 (Table 5). During this study no chicks were observed on lakes where a nest had not been previously located during the current breeding season.

Table 5. Lakes monitored during field survey efforts 2004-2005.

Study Lakes	Monitored in 2004	Confirmed Nesting 2004	Monitored in 2005	Confirmed Nesting 2005
Rogers	X	X	X	X
Lone	X	X	X	X
Monroe	X	X	X	X
Ashley	X	X	X	X
Little Bitterroot	X		X	
McGregor	X		X	
Little McGregor	X		X	
Lost	X			
Lower Thompson	X		X	
Middle Thompson	X		X	
Upper Thompson (East)	X	X	X	X
Upper Thompson (Island)	X	X	X	X
Upper Thompson (West)	X		X	
Loon	X		X	
Horseshoe	X		X	
Crystal	X		X	
Island	X	X	X	X
Lynch	X		X	
Blanchard	X	X	X	X
Boyle	X	X	X	X

Table 5 cont. Lakes monitored during field survey efforts 2004-2005

Study Lakes	Monitored in 2004	Confirmed Nesting 2004	Monitored in 2005	Confirmed Nesting 2005
Beaver	X		X	
Little Beaver	X		X	
Murray	X			
Spencer	X		X	
Skyles	X			
Tally	X	X	X	X
Bootjack	X	X	X	X
Lower Stillwater	X	X	X	X
Upper Stillwater	X	X	X	X
Meadow	X		X	
Upper Whitefish	X		X	
Dog	X	X	X	X
Winona	X	X	X	X
Garnet/Mud	X	X	X	X
Spoon Lake	X	X	X	X
Tepee	X	X	X	X
Cedar Creek	X		X	X
Dickey	X	X	X	X
Murphy	X	X	X	X
Martin	X	X	X	
Bull	X	X	X	X
Gayle's	X	X	X	X
Frank	X	X	X	X
Marl	X	X	X	X
Lick	X	X	X	X
Loon	X	X	X	X
Glen	X		X	

Habitat Characteristics of Nesting Lakes

Loons were observed nesting on lakes that ranged in size from 0.02 to 11.53- km^2 with mean of 1.74- km^2 . The number of homes counted around lakes, and the level of public access, varied among lakes where loons nested (Table 5). VDRSA ranged from 0.00 to 0.664. SDI and MLD ranged from 1.195 to 3.30, and 1.2m to 72.85m, respectively. The number of feeding lakes and breeding pairs within a 10-km radius of a loon nest lake ranged from 1 to 12, and 0 to 7, respectively (Table 6).

Forty-three percent (n=34 nests) of nests located were categorized as shoreline associated, 36.7% of nests (n=29) were on islands, and 20% (n=16) were located on artificial nesting platforms. With respect to vegetation coverage at the nest site, 44.3% of nests (n=35 nests) showed sedge/grass cover, 26.6% (n=21) were covered by reeds, 8.9% (n=7) by shrubs, and the remaining 20.3% represented exposed nests, with no vegetation cover. Thirty percent of nests (n=24) I located were established by loons on MLT territories, 41.8% (n=33) were established on WLT territories, and 27.9% (n=22) of nests were on PLT territories.

Table 6. Mean Estimates of habitat variables measured at loon nesting lakes in Montana, 2004-2005

Covariate	Mean	SE	Range
WTRFL (cm)	1.80	9.14	- 22.9 - 15.2
LSA (sqkm)	1.74	3.22	0.02 -11.5
PERIM (km)	7.14	7.68	0.7 - 26.6
SDI	1.79	0.60	1.2 - 3.3
MLD (m)	8.88	12.48	1.2 - 72.9
VDR(SA)	0.16	0.17	0 - 0.66
VDR(PER)	0.01	0.01	0 - 0.015
MAT	23.23	31.03	0 - 84.0
WD1M (cm)	55.09	73.38	2.0 - 414.0
BP10	3.37	2.06	0 - 7.0
FL10	4.47	3.12	1.0 - 12.0
BPLAKE	1.46	0.84	1.0 - 4.0

A Pearson correlation analysis of continuous variables indicated moderate correlations between several lake scale covariates such as perimeter, shoreline development index and lake surface area. The three disturbance covariates were all highly correlated with one another (Table 7).

Table 7. Pearson correlation coefficients of continuous DSR variables.

	YR	WTRFL	LSA	PERIM	SDI	MLD	VDRSA
YR	1.000						
WTRFL	0.349	1.000					
LSA	-0.045	0.174	1.000				
PERIM	-0.019	0.174	0.908	1.000			
SDI	0.043	0.072	0.352	0.683	1.000		
MLD	-0.028	0.106	0.638	0.554	0.133	1.000	
VDRSA	-0.007	0.028	-0.170	-0.214	-0.118	-0.176	1.000
VDRPER	-0.038	0.138	0.348	0.231	-0.060	0.093	0.794
MAT	-0.059	0.112	0.579	0.473	0.127	0.316	0.499
WD1M	0.009	0.079	-0.120	-0.120	0.014	-0.058	-0.092
BP10	-0.025	0.133	0.256	0.291	0.281	0.119	-0.374
FL10	0.007	-0.019	-0.235	-0.118	0.195	-0.088	0.232
BPLAKE	-0.141	0.126	0.810	0.845	0.507	0.342	-0.017

Table 7. Cont. Pearson correlation coefficients of continuous DSR variables.

	VDRSA	VDRPER	MAT	WD1M	BP10	FL10	BPLAKE
YR							
WTRFL							
LSA							
PERIM							
SDI							
MLD							
VDRSA	1.000						
VDRPER	0.794	1.000					
MAT	0.499	0.800	1.000				
WD1M	-0.092	-0.152	-0.228	1.000			
BP10	-0.374	-0.266	-0.100	0.175	1.000		
FL10	0.232	0.009	0.237	-0.079	-0.202	1.000	
BPLAKE	-0.017	0.388	0.649	-0.175	0.123	-0.024	1.000

Daily Nest Survival and Nesting Success

I examined the candidate sets of a priori models (Table 3) and generated each model's AIC value (Table 8). DSR for common loon nests was best approximated by a priori models within the habitat suite that contained the territory covariate and other lake

scale habitat variables. AIC results from the predation/habitat/disturbance suite also reinforced the effect of TER on DSR, e.g., TER and lake surface area models received strong support. Overall, AIC scores from disturbance models showed that angler days (MAT) had the strongest impact on nest survival among the variables measured.

Table 8. A priori nest survival model results depicting within suite Δ AICc and model weight, as well as combined suited Δ AICc values.

Model	K	Within Suite AICc	Within Suite Δ AICc	Within Suite Wi	Combined Suite Δ AICc
Disturbance suite					
{DSR(SDI + MAT + SDI*MAT)}	4	201.37	0.00	0.799	6.68
{DSR(MAT + NCOV + MAT*NCOV)}	8	204.95	3.58	0.133	10.26
{DSR(MAT)}	2	209.24	7.87	0.016	14.55
{DSR(WD1M + MAT)}	3	209.48	8.11	0.014	14.79
{DSR(VDRPER + NCOV)}	5	210.06	8.68	0.010	15.37
{DSR(LSA + MAT)}	3	211.01	9.63	0.006	16.32
{DSR(SDI + MAT)}	3	211.23	9.86	0.006	16.54
{DSR(VDRPER)}	2	211.47	10.10	0.005	16.78
{DSR(MAT + SDI + NCOV)}	6	212.44	11.06	0.003	17.75
{DSR(LSA + MAT + LSA*MAT)}	4	212.64	11.26	0.003	17.95
{DSR(VDRPER + NCOV + VDRPER*NCOV)}	8	213.11	11.74	0.002	18.42
{DSR(VDRSA + NCOV + VDRSA*NCOV)}	8	214.18	12.81	0.001	19.49
{DSR(VDRSA)}	2	216.27	14.89	0.000	21.58
{DSR(VDRSA + NCOV)}	5	217.09	15.72	0.000	22.40
{DSR(VDRSA + NL + NCOV)}	7	218.41	17.04	0.000	23.72
{DSR(VDRSA + NL + NCOV + YEAR)}	8	219.65	18.28	0.000	24.96
Habitat suite					
{DSR(TER + FL10 + TER*FL10)}	6	194.69	0.00	0.384	0.00
{DSR(TER + BP10)}	4	195.93	1.24	0.207	1.24
{DSR(TER)}	3	196.03	1.34	0.197	1.34
{DSR(TER + BP10 + TER*BP10)}	6	196.87	2.18	0.129	2.18
{DSR(TER + FL10)}	4	197.75	3.06	0.083	3.06
{DSR(WD1M + NL)}	4	212.07	17.37	0.000	17.38
{DSR(PERIM)}	2	214.76	20.07	0.000	20.07
{DSR(WD1M + NL + NCOV)}	7	214.87	20.18	0.000	20.18
{DSR(LSA)}	2	216.06	21.36	0.000	21.37
{DSR(LSA + MLD + SDI)}	4	216.69	21.99	0.000	22.00
{DSR(SDI + PERIM)}	3	216.69	22.00	0.000	22.00

Table 8 cont. A priori nest survival model results depicting within suite Δ AICc and model weight, as well as combined suited Δ AICc values.

Model	K	Within Suite AICc	Within Suite Δ AICc	Within Suite Wi	Combined Suite Δ AICc
{DSR(WTRFL)}	2	217.49	22.80	0.000	22.80
{DSR(SDI)}	2	217.52	22.83	0.000	22.83
{DSR(BP10)}	2	217.62	22.93	0.000	22.93
{DSR(MLD)}	2	218.40	23.71	0.000	23.71
{DSR(FL10)}	2	218.44	23.74	0.000	23.75
{DSR(WTRFL + NL)}	4	220.00	25.31	0.000	25.31
{DSR(WTRFL + NL + WTRFL*NL)}	6	223.44	28.74	0.000	28.75
<hr/> Predation suite					
{DSR(NL + PERIM + NL*PERIM)}	6	214.44	0.00	0.335	19.75
{DSR(PERIM)}	2	214.76	0.32	0.286	20.07
{DSR(NL + PERIM)}	4	216.54	2.10	0.118	21.85
{DSR(YEAR)}	2	217.40	2.96	0.077	22.71
{DSR(SDI)}	2	217.52	3.08	0.072	22.83
{DSR(NCOV)}	4	219.34	4.90	0.029	24.65
{DSR(NL)}	3	219.45	5.01	0.027	24.76
{DSR(SDI + NL)}	4	219.58	5.13	0.026	24.89
{DSR(SDI + NL + SDI*NL)}	6	220.37	5.93	0.017	25.68
{DSR(NL + NCOV)}	6	222.50	8.06	0.006	27.81
{DSR(NL + NCOV + NL*NCOV)}	12	223.46	9.01	0.004	28.77
{DSR(NL + NCOV + YEAR)}	7	224.00	9.56	0.003	29.31
{DSR(MAT + NCOV + NL)}	7	210.78	14.87	0.000	16.09
{DSR(MAT + LSA + WD1M)}	4	211.34	15.43	0.000	16.65
{DSR(MAT + NCOV + LSA)}	6	212.03	16.12	0.000	17.34
{DSR(VDRPER + NCOV + VDRPER*NCOV)}	8	213.11	17.20	0.000	18.42
{DSR(VDRSA + NCOV + VDRSA*NCOV)}	8	214.18	18.27	0.000	19.49
{DSR(NCOV + NL + WD1M)}	7	214.87	18.96	0.000	20.18
{DSR(VDRSA + NCOV + WD1M)}	6	215.51	19.60	0.000	20.82
{DSR(VDRSA + NCOV)}	5	217.09	21.18	0.000	22.40
<hr/> Predation/Habitat Disturbance suite					
{DSR(VDRSA + TER)}	4	195.91	0.00	0.398	1.22
{DSR(VDRPER + TER)}	4	197.24	1.33	0.204	2.55
{DSR(MAT + TER)}	4	198.04	2.13	0.137	3.35
{DSR(MAT + TER + MAT*TER)}	6	198.39	2.49	0.115	3.70
{DSR(VDRSA + TER + VDRSA*TER)}	6	198.44	2.53	0.112	3.75
{DSR(VDRPER + TER + VDRPER*TER)}	6	201.21	5.30	0.028	6.52
{DSR(MAT + NCOV + MAT*NCOV)}	8	204.95	9.04	0.004	10.26
{DSR(VDRPER + NCOV + WD1M)}	6	209.34	13.43	0.000	14.65
{DSR(VDRPER + NCOV)}	5	210.06	14.15	0.000	15.37

Table 8 cont. A priori nest survival model results depicting within suite Δ AICc and model weight, as well as combined suited Δ AICc values.

Model	K	Within Suite AICc	Within Suite Δ AICc	Within Suite Wi	Combined Suite Δ AICc
{DSR(MAT + NCOV)}	5	210.43	14.52	0.000	15.74
{DSR(MAT + NCOV + NL)}	7	210.78	14.87	0.000	16.09
{DSR(MAT + LSA + WD1M)}	4	211.34	15.43	0.000	16.65
{DSR(MAT + NCOV + LSA)}	6	212.03	16.12	0.000	17.34
{DSR(VDRPER + NCOV + VDRPER*NCOV)}	8	213.11	17.20	0.000	18.42
{DSR(VDRSA + NCOV + VDRSA*NCOV)}	8	214.18	18.27	0.000	19.49
{DSR(NCOV + NL + WD1M)}	7	214.87	18.96	0.000	20.18
{DSR(VDRSA + NCOV + WD1M)}	6	215.51	19.60	0.000	20.82
{DSR(VDRSA + NCOV)}	5	217.09	21.18	0.000	22.40

Two exploratory models, based on the best approximating a priori habitat models (i.e., DSR(TER + PERIM), and DSR(TER + SDI)), were selected as the best approximating models to estimate DSR, i.e., their AIC values were nearly equal (Table 9).

Table 9. Combined suite nest survival model results, depicting a priori and exploratory models containing 0.95 of total model weight.

Model	k	AICc	Δ AICc	Wi
{DSR(TER + PERIM)}	4	191.98	0.00	0.271
{DSR(TER + SDI)}	4	192.98	1.01	0.164
{DSR(TER + PERIM + TER*PERIM)}	6	194.29	2.31	0.085
{DSR(TER + FL10 + TER*FL10)}	6	194.69	2.71	0.070
{DSR(TER + LSA)}	4	195.11	3.13	0.057
{DSR(TER + VDRPER + TER*VDRPER)}	3	195.16	3.18	0.055
{DSR(TER + VDRSA)}	4	195.91	3.93	0.038
{DSR(TER + BP10)}	4	195.93	3.95	0.038
{DSR(TER + SDI + TER*SDI)}	6	195.96	3.98	0.037
{DSR(TER)}	3	196.03	4.05	0.036
{DSR(TER + MAT + TER*MAT)}	5	196.38	4.40	0.030
{DSR(TER + BP10 + TER*BP10)}	6	196.87	4.89	0.023
{DSR(TER + VDRPER)}	4	197.24	5.26	0.020
{DSR(TER + FL10)}	4	197.75	5.77	0.015
{DSR(TER + MAT)}	4	198.04	6.06	0.013

I used model averaging to obtain estimates of covariates for models where a model weight was 0.001 or greater. Exploratory models were included in the model averaging procedure. Model averaged beta effects were similar to beta effects from best approximating models (Tables 10 and 11). The 95% confidence intervals on model averaged beta estimates often overlapped zero. These estimates should be viewed as conservative effects of each individual covariate on nest DSR.

Table 10. Model averaged DSR parameter estimates.

Covariate	Beta Estimate	95% CI	
INTERCEPT	1.817	-0.713	4.347
MLT	2.064	0.042	4.087
WLT	1.908	0.152	3.664
PERIM	0.062	-0.253	0.377
SDI	0.697	-0.488	1.882
LSA	0.089	-0.378	0.556
BP10	0.186	-0.590	0.963
FL10	-0.124	-0.847	0.600
VDRPER	-36.193	-49.463	-22.923
VDRSA	-1.741	-3.842	0.359
MAT	-0.008	-0.230	0.214

Table 11. Beta estimates from 5 highest ranking DSR Models.

Model and Model Structure	K	β Estimate	95% CI	
DSR = TER + PERIM				
DSR = $\beta_0 + \beta_1(\text{MLT}) + \beta_2(\text{WLT}) + \beta_3(\text{PERIM})$	4	$\beta_0 = 1.46$	0.599	2.320
		$\beta_1 = 2.83$	1.705	3.954
		$\beta_2 = 2.43$	1.496	3.362
		$\beta_3 = 0.06$	0.013	0.113
DSR = TER + SDI				
DSR = $\beta_0 + \beta_1(\text{MLT}) + \beta_2(\text{WLT}) + \beta_3(\text{SDI})$	4	$\beta_0 = 0.79$	-0.735	2.319
		$\beta_1 = 2.53$	1.478	3.560
		$\beta_2 = 2.23$	1.323	3.135
		$\beta_3 = 0.74$	0.067	1.406
DSR = TER + PERIM + TER*PERIM				
DSR = $\beta_0 + \beta_1(\text{MLT}) + \beta_2(\text{WLT}) + \beta_3(\text{PERIM}) + \beta_4(\text{MLT*PERIM}) + \beta_5(\text{WLT*PERIM})$	6	$\beta_0 = 1.54$	0.657	2.431
		$\beta_1 = 1.85$	-0.859	4.569
		$\beta_2 = 1.51$	-0.365	3.379
		$\beta_3 = 0.06$	0.006	0.108
		$\beta_4 = 0.50$	-0.908	1.904
		$\beta_5 = 0.18$	-0.165	0.524
DSR = TER + FL10 + TER*FL10				
DSR = $\beta_0 + \beta_1(\text{MLT}) + \beta_2(\text{WLT}) + \beta_3(\text{FL10}) + \beta_4(\text{MLT*FL10}) + \beta_5(\text{WLT*FL10})$	6	$\beta_0 = 3.39$	2.085	4.691
		$\beta_1 = 0.04$	-1.805	1.888
		$\beta_2 = 0.26$	-1.451	1.981
		$\beta_3 = -0.18$	-0.398	0.043
		$\beta_4 = 0.48$	-0.011	0.973
		$\beta_5 = 0.34$	-0.029	0.715
DSR = TER + LSA				
DSR = $\beta_0 + \beta_1(\text{MLT}) + \beta_2(\text{WLT}) + \beta_3(\text{LSA})$	4	$\beta_0 = 2.04$	1.386	2.703
		$\beta_1 = 2.35$	1.318	3.385
		$\beta_2 = 2.09$	1.213	2.983
		$\beta_3 = 0.09$	-0.019	0.199

Models that ranked within 5 AIC units of the best approximating models contained TER as a leading predictor variable, suggesting territory had main effects on loon DSR in Montana, yet a single variable model (DSR(TER)) ranked low ($\Delta \text{AICc} = 4.0477$) in the candidate set (Table 9).

The hypothesized negative effect of human development and recreation was not explicitly apparent when disturbance models were combined with other model types, however; models incorporating human disturbance and territory type did receive moderate support, for example, model DSR(VDRPER+TER+VDRPER*TER) ranked 6th among the models evaluated ($\Delta \text{AICc} = 3.1816$). In addition, single predictor models containing human disturbance effects received little support (ΔAICc scores > 17.2605 , Appendix A). Although disturbance effects were not strongly supported in single variable models, MAT was present in all models within 8 AIC units of the most strongly supported model. Most disturbance covariates entered the model list > 8 AIC units from the best model.

Exploratory Data Analysis

During the exploratory analysis, (Table 4) the model DSR(TER+PERIM) was ranked as the best approximating model (Table 11 and 12). DSR estimates were derived for each territory type by running model DSR(TER + PERIM) using the mean, minimum, and maximum perimeter values for each of the three territory types (Table 13). Nests classified as multiple lake territories (MLT's) had daily survival rates of 0.988 (95% CI = 0.973 - 0.995), whole lake territories (WLT's) yielded daily survival rates of 0.986 (95%

CI = 0.973 - 0.993), and DSR at partial lake territories (PLT's) was 0.919 (95% CI = 0.874 - 0.949). There was a slight positive effect of shoreline perimeter (PERIM), $\beta = 0.0631$ (95% CI = 0.0129-0.113). The second most parsimonious model, DSR(TER+SDI) ($\Delta AICc=1.0056$), showed support for a positive effect of shoreline development index (SDI), $\beta = 0.737$ (95% CI = 0.067-1.406) on DSR (Table 11).

Exploratory models containing interaction terms between TER and PERIM, as well as TER and SDI did not improve model fit, (Table 9). Three models containing FL10 and BP10 were present within 5 AIC units of the best model. All three models showed weak positive relationships between FL10, BP10 and DSR.

Table 12. Exploratory nest survival model results.

Model	K	AICc	$\Delta AICc$	Wi
<u>Exploratory suite</u>				
{DSR(TER + PERIM)}	4	191.98	0.00	0.271
{DSR(TER + SDI)}	4	192.98	1.01	0.258
{DSR(TER + PERIM + TER*PERIM)}	6	194.29	2.31	0.134
{DSR(TER + LSA)}	4	195.11	3.13	0.089
{DSR(TER + SDI + TER*SDI)}	6	195.96	3.98	0.058
{DSR(TER + FL10 + BP10+ FL10*BP10)}	6	198.18	6.20	0.019
{DSR(TER + LSA + TER*LSA)}	6	198.49	6.51	0.016
{DSR(BPLAKE)}	2	207.27	15.29	0.001

Table 13. Nest daily survival estimates over a mean, minimum, and maximum lake perimeter in each territory type.

Territory Type		Lake Perimeter (km)	DSR (SE)	95% CI
MLT	(mean)	1.8	0.988 (0.005)	0.973 - 0.995
	(minimum)	0.7	0.987 (0.005)	0.971 - 0.994
	(maximum)	2.6	0.988 (0.005)	0.975 - 0.995
WLT	(mean)	5.5	0.986 (0.005)	0.973 - 0.993
	(minimum)	2.3	0.983 (0.006)	0.966 - 0.991
	(maximum)	13.5	0.991 (0.003)	0.981 - 0.996
PLT	(mean)	15.4	0.919 (0.019)	0.874 - 0.949
	(minimum)	3	0.839 (0.051)	0.712 - 0.916
	(maximum)	26.6	0.958 (0.016)	0.912 - 0.981

Territorial Characteristics of Loon Nests

At the nest site scale, water depth 1-m from the nest (WD1M) was deepest on MLT territories (67.0 cm), followed by WLT territories (61.5cm), and shallowest on PLT territories (32.5 cm) (Table 14). The majority (58.3%) of MLT lake nests were closely associated with the shoreline environments, while nests on PLT lakes were divided among the three nest locations (36.4% shoreline associated, 39.4% on islands, and 24.2% on artificial platforms). PLT lakes contained 36.4% of nests associated with shoreline, 40.9% of nests on islands and 22.7% on artificial platforms. Most (54.2%) of MLT lake nests and 59.1% of PLT lake nests contained sedge and grass as the dominant cover type around the nest. Nest cover on WLT lakes was more diverse, with 27.3% of nests showing sedge and grass cover, 33.3% had cattail and reeds as the dominant cover type, 9.1% with shrub cover, and 30.3 % contained no cover (Table 15).

Table. 14. Gradient of continuous covariate conditions when separated by territory type.

Covariate	MLT (n=24)		Territory Type WLT (n=33)		PLT (n=22)	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Nest Scale						
WD1M (cm)	67.008	93.9	61.46	77.3	32.55	21.941
Lake Scale						
WTRFL	-0.417	2.9	1.12	3.3	1.32	2.8
LSA (sqkm)	0.13	0.1	1.03	1.1	4.57	5.0
PERIM (km)	1.84	0.6	5.51	2.7	15.37	10.0
SDI	1.46	0.2	1.70	0.4	2.28	0.8
MLD	2.84	1.3	10.58	16.5	12.91	10.0
VDR(SA)	0.09	0.1	0.19	0.2	0.19	0.2
VDR(PER)	0.001	0.0	0.006	0.005	0.008	0.005
MAT	1.38	4.7	17.56	20.2	55.57	35.2
BPLAKE	1.00	0.0	1.00	0.000	2.64	0.8
Landscape Scale						
BP10	3.04	2.095	3.697	2.2	3.23	1.8
FL10	4.21	3.647	4.121	3.1	5.27	2.4

Table 15. Gradient of categorical covariate conditions when separated by territory type.

Covariate	MLT (n=24)		Territory Type WLT (n=33)		PLT (n=22)	
	% of Nests	N	% of Nests	N	% of Nests	N
Nest Location						
Shoreline	58.3	14	36.4	12	36.4	8
Island	29.2	7	39.4	13	40.9	9
Platform	12.5	3	24.2	8	22.7	5
Nest Cover						
Sedge/grass	54.2	13	27.3	9	59.1	13
Cattail/Reid	20.8	5	33.3	11	22.7	5
Shrub	8.3	2	9.1	3	9.1	2
None	16.7	4	30.3	10	9.1	2

Water fluctuation during incubation was smallest on MLT territories and highest on PLT territories (Table 14). MLT territories had the smallest mean lake surface area, shortest perimeters, low shoreline development, and lowest mean depth among the three territory types that I observed. PLT territories possessed the largest mean lake surface area, mean perimeter, shoreline development and mean lake depth. Vermeer disturbance ratios (surface area) were lowest on MLT territories (0.087, S.E. 0.0895), followed by WLT territories (0.186, S.E. 0.1922), and highest on PLT territories (0.191, S.E. 0.1777). Vermeer disturbance ratios (perimeter) were lowest on MLT territories, moderate on WLT territories and highest on PLT territories (Table 1.14). Mean angler trips (MAT) showed the greatest difference between territory types. MLT territories had the lowest mean (MAT) values of 1.375 (S.E. 4.6584). Intermediate mean angler trip values were present on WLT territories (17.561, S.E. 20.1536). The highest mean value of (MAT) was observed on PLT territories (55.568, S.E. 35.236) (Table 14). There was no discernable difference between the number of feeding lakes (FL10) and breeding pairs (BP10) within a ten kilometer radius of the nest site when the covariates were broken out by territory type.

The mean number of breeding pairs present on a nest lake showed greatest difference among territories for all measured covariates. As expected by territory definition, all MLT and WLT lakes contained only one loon pair (mean = 1.00, S.E. = 0.00). PLT lakes yielded a mean of 2.6 pairs per lake (S.E. = 0.786). An exploratory model of the number of breeding pairs per lake, DSR(BPLAKE), (ΔAIC_c 15.287)

produced a strongly negative effect on DSR as the number of breeding pairs increased (beta = -0.602, 95% CI = -0.923 - -0.282).

DISCUSSION

The results demonstrated complex relationships between the independent variables I observed and daily survival rate of common loon nests in Northwest Montana. I found a strong effect of territory type, lake perimeter, and the shoreline development index on daily nest survival (Table 11). Lake perimeter and shoreline development (SDI) were highly correlated and the top ranked models indicated that DSR increases as perimeter, or the shoreline development increased in any territory type. I conclude that increased perimeter or shoreline development indices provided loons with greater nest site options, and furthermore, speculate that an increase in shoreline habitat complexity may increase time required for a predator to detect and exploit loon nest sites.

The highest DSR in the study occurred on multi-lake territories (MLT's), a result that seems contradictory to previous research in the eastern U.S. and the upper Great Lakes region. Traditionally, researchers used territory fidelity to assess territory quality, ranking MLT the lowest and WLT the highest quality territories. Ever's (2001) ranking of territory type derived from the assumption that loons on WLT territories need not move to nearby lakes to forage, and thus may avoid territorial conflicts. In contrast, PLT territories may show greater overlap among pairs, which might increase the frequency of territorial conflicts. In contrast, loons nesting on MLT territories potentially defend more than one lake to procure sufficient forage resources, thus representing a territorial lake cluster across the greater landscape.

The results of my analysis provide evidence that loon DSR decreased as the number of nesting pairs on a lake increased. I consider three potential hypotheses to

explain this result, first, when only one nesting pair is present on a lake, the pair will first occupy the most desirable nesting habitat on the lake. As more pairs move in and establish territories on the same lake, each new territory is located in less desirable habitat than the previous territory (Fretwell and Lucas 1970). Second, late arriving pairs that establish a territory may be young birds just entering the breeding population, with limited or no previous nesting experience, hence overall DSR would drop. Third, territory intrusions from neighboring loons were more common on lakes with two or more nesting pairs than on lakes with a single pair, thus enclaves may attract competitors, and aggressive defense and physical conflicts, or visual and vocal displays, could reduce DSR

The number of loon pairs observed on PLT lakes within the study area appears to be increasing. Observations of loon density increases have been associated with declines in both site fidelity and long term reproductive success (Evers 2002). Although PLT lakes hosted numerous breeding pairs, they had the lowest DSR among territory types I observed, and these results suggest PLT lakes represent population sinks, or sites for “floaters” (Rodenhouse et al. 1997), temporarily housing excess breeding birds until a more productive MLT lake becomes available.

Conversely, MLT lakes might have high DSR due in part to a release from predation pressure. During some nest visits to MLT lakes a single incubating adult was observed, with the mate absent from the nest vicinity or absent from the lake. Multi-lake foraging by one member of the pair could reduce vocalizations and other predator attracting activities in the nest area, thus reducing the rate of cues given to predators.

When activities such as foraging or territorial conflicts occur on smaller MLT lakes, loon activity was often spread over the entire lake area rather than concentrated near a nest site. Dispersed activity could disrupt the ability of predators to locate the nest site. The increased loon activity on PLT lakes, including territorial conflicts, incubation exchanges, and vocalizations could cause increased predator awareness and increased nest search effort, particularly by avian predators such as common ravens (*Corvus corax*) and bald eagles (*Haliaeetus leucocephalus*). Because of relatively large lake surface areas on WLT and PLT lakes, foraging and territorial conflicts are more likely to occur near the nest site providing stronger predator cues to the nest location.

Loons that nest on multi-lake territories may experience higher daily nest survival rates as a greater number of foraging lakes occur within a 10-km radius. Adjacent foraging lakes may provide loons with more energy efficient foraging conditions than the breeding lake as well as reduce the amount of time loons are visible near a nest. Loons nesting on larger whole-lake territories or partial-lake territories may be less dependent on food sources from other nearby lakes. I hypothesize that physical lake characteristics may interact with human-use to create a complex set of effects on daily nest survival. For example, small lakes with less complex shoreline and littoral zone habitats will be impacted more by slight increases in recreation and development than large lakes that provide greater habitat diversity and a greater number of potential nest sites.

While the combination of habitat characteristics and the number of breeding pairs per lake appeared to have a significant impact on DSR, there may be other factors

embedded within territory type that affects DSR. To further explore these potential relationships, covariates were sorted by territory type to summarize and compare mean and standard error values (Table 14, Table 15). Although a negative effect from human disturbance was not supported in the AIC analysis, a gradient of human use was apparent when I examined means and standard errors of covariates among lake type. For example, MLT territories had the highest DSR and also the lowest mean values for all disturbance variables. I observed moderate levels of disturbance on WLT lakes and the highest mean values of disturbance covariates were found on PLT lakes (Table 14). At the landscape scale there was no discernable difference in the numbers of breeding pairs and feeding lakes within a 10-km radius of the nesting lake when lakes were categorized by territory, suggesting territory, as defined by Evers (2001), was an effective way to predict DSR in my study area.

Management Implications

The results of my research direct wildlife managers to consider not only lake scale habitat but also landscape level factors, including the distribution and quality of multiple lakes across the landscape. The traditional approach of focusing management toward large lakes and ignoring complex multi-lake territories may not be sufficient for loon persistence in Montana. Management priorities for all three territory types should focus on maintaining and restoring current shoreline and island nesting habitat and minimizing watercraft recreation using methods such as temporary “no wake” restrictions during the nesting period. Small nesting lakes (MLT territories) were the most

productive and should receive the highest attention. Management actions on MLT lakes need to consider minimizing watercraft disturbance on nearby lakes to improve foraging habitat for loons. Minimizing surface area disturbances on potential forage lakes surrounding MLT lakes may maximize foraging efficiency allowing adults to quickly catch enough fish to meet energy requirements and reduce the number of lakes needed to support a MLT pair. Many MLT lakes are privately owned or currently have limited access, thus communications with landowners regarding land-use options around private lakes is essential. My results highlight the need for continued research from a landscape scale approach. More detailed investigations about the nest survival of different territory types in relation to different landscape level factors are essential. Research about forage lake characteristics of MLT lakes is needed to guide forage lake protection efforts to maintain the future productivity of MLT lakes.

FACTORS AFFECTING COMMON LOON CHICK SURVIVAL IN NORTHWEST MONTANA

Introduction

During the 1980s, numerous field studies documented habitat characteristics associated with Common Loon (*Gavia immer*) brooding sites (McIntyre 1983, Strong and Bissonette 1989). Observations of brood chicks in Maine and northern Saskatchewan revealed that chicks spent most of their time in shallow water (< 2-m depth) within 150-m from shore. Chicks primarily used small bays and coves which may have provided protection from wind driven waves (Strong and Bissonette 1989). Strong and Bissonette (1989) also observed chicks moving to shorelines with emergent vegetation when adults gave distress calls, and Yonge (1981) observed that chicks hid within shoreline vegetation when threatened by predation.

A variety of factors have been shown to influence loon chick survival rates, e.g., increased boat traffic may cause chicks to spend more time swimming to avoid boat traffic and less time feeding and resting (Christenson 1981). Variation in time spent back riding and resting, versus engaged in avoidance swimming, was associated with changes in fledging rates (Nocera et al. 1998). Chicks that spend less time feeding and more time swimming and moving may have lower survival. Chick energy requirements are especially high when compared to those of other birds during their first four weeks of life, and energy requirements tend to peak just before fledging at 10-13 weeks. Fournier (2002) speculated the high energy requirement may be due to an inability of young chicks

to efficiently thermo-regulate, and back-riding may facilitate thermoregulation by keeping young chicks dry. Mortality reported for chicks after 4 weeks of age is so rare that reproduction has been considered successful after that period (Yonge 1981).

Although Evers (2002) observed that chick mortality after six weeks was less than 5%, I hypothesized that chick mortality may increase after four weeks when chicks become independent and spend more time away from adults, thus increasing vulnerability to predation.

research investigating loon chick survival and chick rearing habitat has not been conducted in Montana. Effects of habitat modifications and human disturbance on chick survival rates are unknown while anthropogenic modifications to habitat appear to be increasing, particularly in highly desirable lake-side settings. Human lakeshore development and water based recreation activities could negatively affect loon chick survival. Because loons are slow to pioneer or re-colonize habitats, repeated nest failures might result in population fragmentation and local extinctions. Increasing isolation of small populations can further reduce gene flow between subpopulations and exacerbate loss of genetic diversity (Pannell and Charlesworth 2000).

Identifying threats to loon nesting and foraging habitat in Montana is a key requirement for long-term management. Because the effects of recreation activity on loon chick survival are unknown, research investigating chick survival rates in Montana seems warranted. Recreation and home building on nesting lakes in northwest Montana have increased dramatically in the last decade (www.flatheadbasincommission.org). Current and historic nesting lakes comprise a complex mosaic of habitat conditions, and

the relationship among habitat type, human disturbance, and chick survival remains uncertain. Current management strategies involve organized surveys to monitor abundance of adults and young (Bissell, 2005).

To date, the only existing information on loon survival and recruitment rates come from mark/re-sight studies in the Eastern U.S. (Evers 2004). Because both breeding and winter habitats in Montana vary widely from the Eastern U.S., applying documented vital rate and habitat knowledge to loons in Montana may not be adequate. Given the lack of local knowledge on loon population and habitat characteristics, the objectives of this study were to evaluate the relationships between loon chick survival rates and environmental covariates across multiple spatial scales, including investigations of individual lakes, and clusters of lakes across the landscape.

My research on chick survival focused at two spatial scales: lake and landscape. At the lake scale, the primary research questions were: (1) how do physical habitat characteristics affect the magnitude of chick survival among lakes with differing habitat settings? (2) does human disturbance (lakeshore development and recreation) affect chick survival? (3) does human disturbance interact with physical habitat variables to influence variation in chick survival rates? To test the effects of covariates on chick survival I hypothesized: (1) chick survival will be negatively related to lake surface area, (2) there will be a positive effect of shoreline development index (SDI, shoreline complexity) on loon chick survival, and (3) lakes with higher measures of human development and recreation will experience lower chick survival rates than lakes with little or no human development and recreation.

Implicit in my reasoning about lake scale factors that influence chick survival were four assumptions: First, while large lakes are typically deep and provide abundant space for medium to large size prey fish for adult loons, larger lakes may lack diversity in the littoral zone habitats preferred for chick rearing. Diversity could be important because common prey like yellow perch (*perca flavescens*), leeches (*Hirudinidae*), and various crustaceans inhabit shallow littoral zone habitat. Furthermore, larger lakes with deep open water are often dominated by less available Salmonid prey species (Evers 2004). Next, I assumed that lakes with irregular shorelines possess more protected bays and coves for chicks to avoid natural wave action and boat activity. I further assumed that recreation activity would reduce the amount of time chicks spend feeding and resting while increasing energy demands. Finally, I assumed that a decrease in shoreline cover, i.e., live trees and shrubs associated with increased development (Christensen et al. 1996) would reduce chick hiding cover and increase losses to avian predation.

At the landscape scale, my research questions included: (1) does the number of nearby foraging lakes and numbers of adjacent breeding pairs have an effect on chick survival? (2) do adjacent lakes increase forage opportunities or increase the number of territorial conflicts with adults on neighboring lakes? (3) is there an interaction among breeding lake surface area, number of adjacent foraging lakes, the number of breeding pairs within 10-km and loon chick survival? I hypothesized: (1) chick survival rates will be positively related to the number of feeding lakes within a 10-km radius, and the effect will be strongest on small lakes, and (2) loon chick survival will be negatively related to the number of breeding pairs within a 10-km radius of the nesting lake. My hypotheses

were rooted within four assumptions: (1) Numerous adjacent feeding lakes provide breeding adults more forage opportunities, and adjacent lakes also allow adults to forage more efficiently if factors such as human recreation and boat use become too high on the nesting lake. Efficiency refers to the occurrence of feeding bouts with fewer human interferences. A high number of foraging lakes could reduce the frequency of territorial conflicts between other single or non-territory holding loons. (2) Increased nest density may increase the occurrence of territorial conflicts which can result in chick mortality due to physical injury by intruding loons or increased predation and exposure losses due to separation from adults. As nest densities increase, and more lakes are occupied or more pairs settle near existing territories on the same lake, site fidelity, nest success, and chick survival will decline (Evers 2002).

METHODS

Brood Monitoring

Forty-seven lakes were originally selected for monitoring chick survival during the 2004 and 2005 field seasons. These lakes historically hosted breeding loons or showed evidence of use by common loons during the breeding season based on MFWP Loon Day Survey Counts. Three lakes (Lost, Murray, Skyles) were dropped from surveys during the 2005 field season because no loons were observed during 2004. After hatching, brooding loons were highly visible and vocal, spending most of their time in traditional "post fledging areas", called nursery areas. Because of brood conspicuousness, I assumed that chick detection rates were 100% during each lake visit. Each loon chick brood was monitored at 4 day intervals during the first 4 weeks post hatch. Once brood chicks reached 4 weeks of age, broods were monitored twice more at eight day intervals for a total of 9 observations of each brood over a 44 day period. During each observation I recorded the number of chicks observed, adult behavior, weather, and watercraft use and recreation on the lake. Loon family groups were highly visible and vocal so that observations were conducted from a distance using spotting scopes to eliminate potential disturbance. Typical observation distances ranged from 100-m to 300-m. A loon chick was considered to have died if it was not observed during a monitoring event. Chick loss was confirmed by the absence of the chick during two consecutive monitoring efforts.

Habitat covariate data were also collected at two spatial scales, lake and landscape. At the lake spatial scale, the following data will be collected; surface area, mean depth, fish assemblages, and shoreline development index. The shoreline development index (SDI) is a measure of physical lake edge complexity, calculated by:

$$SDI = L/2\sqrt{(\pi A)},$$

where *L* is the length of the shoreline and *A* is the surface area of the lake. SDI is a comparative value relating the shoreline length to the circumference of a circle that has the same area as the lake. The smallest possible value would be 1.0 for the case of a perfectly circular lake. Shoreline irregularities such as bays, coves, inlets, and points result in increased SDI (Cole 1994). Using MFWP data, the presence and abundance of yellow perch and pike were measured. Perch are a preferred prey for loons (Evers, 2004) and pike have been shown to prey on ducklings (Solman 1945) and loon chicks (Yonge 1981).

Finally, I used Montana Fish, Wildlife and Parks angling pressure data (MFWP 2001, 2003) and a technique developed by Vermeer (1973) to classify human disturbance levels on lakes. Many lakes included in this study contained strong populations of Northern Pike and Large Mouth Bass. Fishing pressure for these species can be intense during May and June when loons are nesting. Montana angler pressure reports are compiled biannually for the summer and winter fishing seasons. The 2001 and 2003 angler pressure reports were the most current available at the time to data analysis. I averaged the angler trips during summer 2001 and summer 2003 angling seasons to obtain the mean angler trips (MAT) covariate value for each lake. Angler trip numbers

from 2001 and 2003 were similar for individual lakes between years and were expected to represent a reasonable measure of angler use during the 2004 and 2005 study seasons. To calculate Vermeer disturbance ratios, ten disturbance units were assigned to each government campsite and resort, 5 points for each unmaintained public access site, and 1 disturbance unit for each house and summer home bordering the lake. The total number of disturbance units calculated for each lake was then divided by the lake surface area to obtain the disturbance ratio in relation to surface area (VDRSA). I also divided the number of disturbance points by the lake perimeter to calculate VDRPER. As an example, a lake with 3 homes (3 points), 1 public boat launch (10 points), and 2 unmaintained public access sites (10 points) with 250 acres of surface water and a perimeter of 4300 meters would have the following disturbance index:

$$\text{VDR(SA)} = (3 + 10 + 10) / 250 = 0.0920;$$

$$\text{VDR(PER)} = (3 + 10 + 10) / 4300 = .0053.$$

Three landscape scale habitat variables were measured for each loon brood: (1) the number of breeding pairs located within a 10-km radius from the nest (BP10); (2) the number of feeding lakes larger than 8-ha and not occupied by an established breeding loon pair) within 10-km radius from the nest (FL10); and (3) territory type based on Evers (2001) territory classification selected to investigate the relationships between nesting lake size, multiple lake use by adults, and the effects on DSR of having multiple nesting pairs per lake in response to territoriality and potential density dependent effects (Table 16).

Table 16. Common Loon chick survival variables measured during field research with abbreviations and definitions.

Covariate	Definition
ATSA	Mean angler trips divided by lake surface area
BP10	Number of breeding loon pairs within 10 km radius of the nesting lake
FL10	Number of feeding lakes (lakes without breeding pairs) within 10 km radius of the nest
HD	Hatch date
LSA	Lake surface area
MAT	Mean angler trips
MLD	Mean lake depth
PERIM	Shoreline perimeter
PIKE	Presence or absence of Northern Pike
SDI	Shoreline development index (measure of shoreline complexity)
VDR(PER)	Vermeer disturbance ratio (development and recreation use of the lake in relation to lake perimeter)
VDR(SA)	Vermeer disturbance ratio (development and recreation use of the lake in relation to lake surface area)
YP	Yellow Perch density
YR	Year

Data Analysis

A priori candidate model suites were constructed in three categories based on the hypothesized effects of covariates on chick survival (Table 17). I constructed a predation suite, habitat suite, and human disturbance suite, as predation, habitat, and human disturbance are the three main factors most expected to affect chick survival (Table 18). I started by building single predictor models, and then added models containing combinations of biologically relevant covariates. Finally, I added models containing biologically relevant covariates which may interact to influence nest survival.

Table 17. Hypothesized covariate effects on common loon chick survival.

Scale	Covariate	Covariate Subtype	Effect (slope)
<u>Lake</u>	LSA		$\beta < 0$
	SDI		$\beta > 0$
	MLD		$\beta < 0$
	VDR(SA)		$\beta < 0$
	VDR(PER)		$\beta < 0$
	Pike		$\beta < 0$
	YP		$\beta > 0$
	MAT		$\beta < 0$
	AT/SA		$\beta < 0$
<u>Landscape</u>	BP10		$\beta < 0$
	FL10		$\beta > 0$
	TER	Whole Lake	$\beta > 0$
		Partial Lake	$\beta < 0$
		Multiple Lake	$\beta < 0$

Table 18. A priori chick survival model list.

Model	Model Structure
<u>Disturbance suite</u>	
{S(VDRPER)}	$S = B_0 + B_1(\text{age}) + B_2(\text{VDRPER})$
{S(ATSA)}	$S = B_0 + B_1(\text{age}) + B_2(\text{ATSA})$
{S(HD)}	$S = B_0 + B_1(\text{age}) + B_2(\text{HD})$
{S(VDRSA)}	$S = B_0 + B_1(\text{age}) + B_2(\text{VDRSA})$
{S(MAT)}	$S = B_0 + B_1(\text{age}) + B_2(\text{MAT})$
{S(YEAR)}	$S = B_0 + B_1(\text{age}) + B_2(\text{YEAR})$
{S(HD+VDRPER)}	$S = B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{VDRPER})$
{S(HD+VDRSA)}	$S = B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{VDRSA})$
{S(SDI+MAT)}	$S = B_0 + B_1(\text{age}) + B_2(\text{SDI}) + B_3(\text{MAT})$
{S(HD+MAT)}	$S = B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{MAT})$
{S(LSA+MAT)}	$S = B_0 + B_1(\text{age}) + B_2(\text{LSA}) + B_3(\text{MAT})$
{S(SDI+MAT+SDI*MAT)}	$S = B_0 + B_1(\text{age}) + B_2(\text{SDI}) + B_3(\text{MAT}) + B_4(\text{SDI*MAT})$
{S(HD+VDRSA+SDI)}	$S = B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{VDRSA}) + B_4(\text{SDI})$
{S(HD+VDRPER+HD*VDRPER)}	$S = B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{VDRPER}) + B_4(\text{HD*VDRPER})$

Table 18 cont. A priori chick survival model list.

Model	Model Structure
{S(HD+VDRSA+HD*VDRSA)}	$S=B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{VDRSA}) + B_4(\text{HD} * \text{VDRSA})$
{S(LSA+MAT+LSA*MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{LSA}) + B_3(\text{MAT}) + B_4(\text{LSA} * \text{MAT})$
{S(HD+MAT+HD*MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{MAT}) + B_4(\text{HD} * \text{MAT})$
Habitat suite	
{S(FL10)}	$S=B_0 + B_1(\text{age}) + B_2(\text{FL10})$
{S(BP10)}	$S=B_0 + B_1(\text{age}) + B_2(\text{BP10})$
{S(SDI)}	$S=B_0 + B_1(\text{age}) + B_2(\text{SDI})$
{S(HD)}	$S=B_0 + B_1(\text{age}) + B_2(\text{HD})$
{S(LSA)}	$S=B_0 + B_1(\text{age}) + B_2(\text{LSA})$
{S(FL10+BP10)}	$S=B_0 + B_1(\text{age}) + B_2(\text{FL10}) + B_3(\text{BP10})$
{S(YP)}	$S=B_0 + B_1(\text{age}) + B_2(\text{YP})$
{S(SDI+MLD)}	$S=B_0 + B_1(\text{age}) + B_2(\text{SDI}) + B_3(\text{MLD})$
{S(LSA+MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{LSA}) + B_3(\text{MAT})$
{S(FL10+BP10+FL10*BP10)}	$S=B_0 + B_1(\text{age}) + B_2(\text{FL10}) + B_3(\text{BP10}) + B_4(\text{FL10} * \text{BP10})$
{S(SDI+MLD+SDI*MLD)}	$S=B_0 + B_1(\text{age}) + B_2(\text{SDI}) + B_3(\text{MLD}) + B_4(\text{SDI} * \text{MLD})$
{S(LSA+MAT+LSA*MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{LSA}) + B_3(\text{MAT}) + B_4(\text{LSA} * \text{MAT})$
{S(SDI+MLD+YP)}	$S=B_0 + B_1(\text{age}) + B_2(\text{SDI}) + B_3(\text{MLD}) + B_4(\text{YP})$
Predation suite	
{S(.)}	$S=B_0$
{S(SDI)}	$S=B_0 + B_1(\text{age}) + B_2(\text{SDI})$
{S(HD)}	$S=B_0 + B_1(\text{age}) + B_2(\text{HD})$
{S(MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{MAT})$
{S(YEAR)}	$S=B_0 + B_1(\text{age}) + B_2(\text{YEAR})$
{S(SDI+MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{SDI}) + B_3(\text{MAT})$
{S(HD+YEAR)}	$S=B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{YEAR})$
{S(PIKE+VDRSA)}	$S=B_0 + B_1(\text{age}) + B_2(\text{PIKE}) + B_3(\text{VDRSA})$
{S(LSA+MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{LSA}) + B_3(\text{MAT})$
{S(HD+HD^2)}	$S=B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{HD} * \text{HD})$
{S(SDI+MAT+SDI*MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{SDI}) + B_3(\text{MAT}) + B_4(\text{SDI} * \text{MAT})$
{S(HD+YEAR+HD*YEAR)}	$S=B_0 + B_1(\text{age}) + B_2(\text{HD}) + B_3(\text{YEAR}) + B_4(\text{HD} * \text{YEAR})$
{S(PIKE+VDRSA+PIKE*VDRSA)}	$S=B_0 + B_1(\text{age}) + B_2(\text{PIKE}) + B_3(\text{VDRSA}) + B_4(\text{PIKE} * \text{VDRSA})$
{S(LSA+MAT+LSA*MAT)}	$S=B_0 + B_1(\text{age}) + B_2(\text{LSA}) + B_3(\text{MAT}) + B_4(\text{LSA} * \text{MAT})$

Chick survival models were evaluated using the known fate module of Program MARK (Cooch and White 1999). The 9 encounter occasions were grouped into 4 occasions to smooth the uncertainty of age which can be ± 4 days as a result of nest monitoring intervals. The 4 resulting intervals were not equal, with interval one encompassing hatching to 8 days old, interval two 9-16 days, interval three 17-28 days, and interval four covered day 29-44. Covariate models were run with a design matrix that allowed individual covariates with different intercepts and slopes during the first time interval and the following three intervals. This resulted in two survival rates, 1 during the first time interval (0-8 days) and a second encompassing the final three time intervals (9-44 days).

Traditionally, investigators used sequential null hypothesis tests or step-wise procedures to screen habitat data for significant variables to develop predictive models. This use of null-hypothesis testing as a data-mining tool has been criticized for unsound inference (Chatfield 1995, MacNally 2000, Royall 1997, Burnham and Anderson 2002). Akaike's information criterion (AIC) provides an alternative to traditional analyses to evaluate habitat associations. AIC estimates the amount of information lost when using a particular model to approximate reality compared with other models; better models lose less information (Burnham and Anderson 2002). Because results depend on the entire set of candidate models, all models should be identified before data analysis. In exploring species-habitat associations, AIC methods can quantify the relative importance of habitat variables, provide evidence for association, and identify combinations of variables best used for prediction. Information theoretic approaches use AIC values and the concept

of parsimony to rank best approximating models. I examined AIC model weights to evaluate evidence in support of a particular model compared to other models in the candidate list. I used model averaging to derive slope estimates for predictive models. I assumed the fate of an individual nest to be independent of other nest fates and I examined diagnostic tests for evidence of over dispersed data (Dinsmore et al. 2002).

My modeling approach incorporated existing data combined with data collected during field investigations. Literature about loon chick rearing habitat, as well as studies that documented effects of human disturbance on chick survival inspired the hypothesized habitat-chick survival associations (Table 17). The stated hypotheses led to the construction of candidate lists of a priori models (Table 18). Candidate models were divided among hypothesized suites of habitat factors, including (1) models associated with the effects of human disturbance on survival; (2) habitat-based covariates; (3) models exploring predation effects, and (4) exploratory combinations of the first three suites that might represent the best approximating model (Table 19) (Burnham and Anderson 2002). Selection of the best approximating model for chick survival was evaluated using the known fate module in Program MARK (White and Burnham 1999).

Table 19. Exploratory chick survival model list.

Model	Model Structure
Exploratory suite	
{S(MAT+FL10+BP10)}	$S = B_0 + B_1(\text{age}) + B_2(\text{MAT}) + B_3(\text{FL10}) + B_4(\text{BP10})$
{S(MAT+FL10+BP10+FL10*BP10)}	$S = B_0 + B_1(\text{age}) + B_2(\text{MAT}) + B_3(\text{FL10}) + B_4(\text{BP10}) + B_5(\text{FL10} * \text{BP10})$
{S(LSA +FL10+BP10+FL10*BP10)}	$S = B_0 + B_1(\text{age}) + B_2(\text{LSA}) + B_3(\text{FL10}) + B_4(\text{BP10}) + B_5(\text{FL10} * \text{BP10})$
{S(VDRSA+FL10+BP10+FL10*BP10)}	$S = B_0 + B_1(\text{age}) + B_2(\text{VDRSA}) + B_3(\text{FL10}) + B_4(\text{BP10}) + B_5(\text{FL10} * \text{BP10})$
{S(4ages)FL10+BP10+FL10*BP10)}	$S = B_0 + B_1(\text{age1}) + B_2(\text{age2}) + B_3(\text{age3}) + B_4(\text{age4}) + B_5(\text{MAT}) + B_6(\text{FL10}) + B_7(\text{BP10}) + B_8(\text{FL10} * \text{BP10})$

The global model was tested for overdispersion (\hat{c}) because the fate of a chick may not be independent from the fate of its brood mate. Overdispersion was estimated by dividing the model's deviance by its degrees of freedom. An overdispersion factor (\hat{c}) of 1.0 indicates the fate of brood mates were totally independent. Since this method is known to be biased high, in some cases as much as 15%, (Cooch and White 1999) I raised the default \hat{c} value of all models from 1.00 to 1.50.

Models were ranked based on Akaike's Information Criterion (AIC) and adjusted for small sample size (AICc) and overdispersion (QAICc). AIC allows for the comparison of non-nested models. This method uses parsimony to select the simplest model that best explains the survival data collected. AIC penalizes a model as the number of parameters increase, thus finding the best combination between bias and variance. The model in the candidate list with the lowest AIC score is considered to be the most parsimonious model. I also examined the Akaike model weight when examining model selection results. This is a measure of the weight of evidence in support of a particular model compared to the other models in the candidate list.

To better understand how landscape effects might interact with lake surface area (LSA) and human disturbance factors, I conducted exploratory analysis by building five models based on the best a priori model (Table 19). I also ran the best a priori model allowing chick survival to differ in each of the four time intervals. These exploratory models can be used to generate hypotheses for future research and guide the collection of covariate data at multiple spatial scales.

RESULTS

Seventy-nine nesting attempts were monitored during the two field seasons. All nests were monitored until the nest either hatched or failed. Twenty-four successful nesting attempts produced 37 chicks on 22 different lakes in 2004. Seventeen successful nesting attempts produced 28 chicks on 17 different lakes in 2005. I recorded 65 chicks hatched on my study lakes, 50 of the 65 (77%) survived the 44 day observation period.

Habitat Conditions of Lakes Supporting Common Loon Broods

Successful nesting lakes that produced chick broods for monitoring ranged in size from 0.020 to 4.90 km², with a mean size of 0.844 km². The number of homes and public accesses spanned a wide gradient across lakes, resulting in Vermeer disturbance ratios (surface area disturbance ratio) ranging from 0.00 to 0.664, and perimeter disturbance ratio from 0.000 to 0.0015. Shoreline development indices (SDI) and mean lake depths ranged from 1.195 to 3.30, and 1.2-m to 72.85-m, respectively. The number of feeding lakes and breeding pairs within a 10-km radius of the nesting lake ranged from 1 to 12, and 0 to 7, respectively (Table 20).

Table 20. Mean estimates of habitat variables measured on lakes with loon broods in Montana, 2004-2005.

Covariate	Mean	S.E.	Range
HD	39.53	14.33	18 – 73
LSA (km ²)	0.84	1.09	0.02 – 4.9
SDI	1.80	0.56	1.20 - 4.90
MLD (m)	8.35	14.19	1.2 - 72.85
VDRSA	0.14	0.15	0 - 0.664
VDRPER	0.38	0.39	0 - 0.0015
MAT	13.70	19.26	0 – 78
AT/SA	2.28	3.53	0 – 129.4
BP10	3.55	2.25	0 – 7
FL10	4.43	3.45	0 – 12

Fish assemblages varied considerably between study lakes. Almost half of the lakes supporting broods (47.8%, n =11 lakes) contained northern pike that may prey on small ducklings or loon chicks (Solman 1945, Yonge 1981). Approximately 34.8% (n=8) of lakes contained abundant yellow perch populations, one lake consisted of low perch population density, and 60.9% of lakes (n=14) supported no yellow perch.

A Pearson correlation analysis of continuous variables indicated moderate correlations between several lake scale covariates, including perimeter, shoreline development index, and lake surface area. The four disturbance covariates were all highly correlated. No significant correlations were observed between covariates within the same model in the highest ranking models (Table 21).

Table 21. Pearson correlation coefficients of continuous chick survival variables.

	HD	YR	LSA	SDI	MLD	VDRSA
HD	1.000					
YR	0.302	1.000				
LSA	0.092	-0.053	1.000			
SDI	0.031	-0.186	0.275	1.000		
MLD	0.095	0.047	0.829	0.011	1.000	
VDRSA	-0.180	-0.021	-0.253	0.160	-0.204	1.000
VDRPER	-0.064	-0.018	-0.078	0.043	-0.171	0.844
MAT	-0.237	0.065	0.139	0.199	0.124	0.605
AT.SA	-0.304	0.075	-0.147	0.180	-0.080	0.618
BP10	0.009	-0.068	-0.054	0.156	-0.022	-0.154
FL10	-0.320	-0.014	0.000	0.218	0.031	0.216

Table 21. cont. Pearson correlation coefficients of continuous chick survival variables.

	VDRPER	MAT	ATSA	BP10	FL10
HD					
YR					
LSA					
SDI					
MLD					
VDRSA					
VDRPER	1.000				
MAT	0.645	1.000			
AT.SA	0.514	0.844	1.000		
BP10	-0.229	-0.046	0.002	1.000	
FL10	0.051	0.546	0.742	-0.056	1.000

Common Loon Chick Survival

Common loon chick survival was parsimoniously predicted by a priori models containing landscape scale covariates. A priori models in the habitat suite containing landscape scale covariates received considerable support (Table 22). These models suggested a strong positive effect on forage lakes and a weak positive effect of breeding pairs on chick survival. There was relatively little support for models containing only lake scale habitat covariates such as SDI, MLD, YP, and LSA. Disturbance suite models offered nearly equal support for all single predictor models. No single disturbance predictor was more highly supported than other disturbance predictors. A priori models containing year received little support. The most parsimonious model containing year was S(YEAR) which yielded a Δ QAICc of 11.377. Models containing hatch data (HD) also received little support.

Based on the strong a priori explanation of effects by landscape covariates, I built a limited suite of exploratory models to investigate the relationships between

foraging lakes, breeding pairs, and disturbance on chick DSR. I combined the exploratory landscape and lake scale model results (Table 23) with all other models in the Chick Survival all models suite (Table 24 and Appendix A). The 6 most parsimonious models contained both landscape scale covariates (i.e., BP10 and FL10) and accounted for 92.6% of the model weight. The landscape model S(FL10 + BP10) ($\Delta\text{QAICc} = 9.119$) was significantly improved with the addition of an interaction term, S(FL10 + BP10 + FL10*BP10) ($\Delta\text{QAICc} = 5.144$).

Table 22. A priori chick survival model results depicting within suite ΔQAICc and model weight, as well as combined suited ΔQAICc values.

Model	K	Within Suite QAICc	Within Suite ΔQAICc	Within Suite Wi	Combined Suite ΔQAICc
Predation suite					
{S(SDI+MAT+SDI*MAT)}	5	73.79	0.00	0.235	4.81
{S(SDI)}	3	75.09	1.30	0.122	6.11
{S(HD)}	3	75.14	1.35	0.120	6.16
{S(MAT)}	3	75.20	1.41	0.116	6.22
{S(YEAR)}	3	75.22	1.43	0.115	6.24
{S(TIME)}	4	76.83	3.04	0.051	7.85
{S(SDI+MAT)}	4	77.12	3.33	0.044	8.14
{S(HD+YEAR)}	4	77.17	3.38	0.043	8.19
{S(PIKE+VDRSA)}	4	77.21	3.42	0.042	8.23
{S(LSA+MAT)}	4	77.24	3.45	0.042	8.26
{S(HD+YEAR+HD*YEAR)}	5	78.10	4.31	0.027	9.12
{S(PIKE+VDRSA+PIKE*VDRSA)}	5	78.56	4.77	0.022	9.58
{S(LSA+MAT+LSA*MAT)}	5	79.10	5.31	0.017	10.12
{S(.)}	1	82.75	8.96	0.003	13.77
Habitat suite					
{S(FL10+BP10+FL10*BP10)}	5	68.98	0.00	0.596	0.00
{S(FL10)}	3	72.72	3.74	0.092	3.74
{S(FL10+BP10)}	4	72.96	3.97	0.082	3.98
{S(BP10)}	3	72.98	4.00	0.081	4.00
{S(YP)}	4	74.60	5.62	0.036	5.62
{S(SDI)}	3	75.09	6.11	0.028	6.11
{S(HD)}	3	75.14	6.16	0.027	6.16
{S(LSA)}	3	75.28	6.29	0.026	6.30
{S(SDI+MLD)}	4	76.99	8.00	0.011	8.01

Table 22 cont. A priori chick survival model results depicting within suite Δ QAICc and model weight, as well as combined suited Δ QAICc values.

Model	K	Within Suite QAICc	Within Suite Δ QAICc	Within Suite Wi	Combined Suite Δ QAICc
{S(LSA+MAT)}	4	77.24	8.26	0.010	8.26
{S(SDI+MLD+YP)}	6	78.70	9.71	0.005	9.72
{S(SDI+MLD+SDI*MLD)}	5	79.01	10.03	0.004	10.03
{S(LSA+MAT+LSA*MAT)}	5	79.10	10.11	0.004	10.12
<hr/>					
Disturbance suite					
{S(SDI+MAT+SDI*MAT)}	5	73.79	0.00	0.184	4.81
{S(VDRPER)}	3	74.91	1.12	0.105	5.93
{S(ATSA)}	3	75.06	1.27	0.098	6.08
{S(HD)}	3	75.14	1.35	0.094	6.16
{S(VDRSA)}	3	75.19	1.40	0.092	6.21
{S(MAT)}	3	75.20	1.41	0.091	6.22
{S(YEAR)}	3	75.22	1.43	0.090	6.24
{S(HD+VDRPER)}	4	76.85	3.06	0.040	7.87
{S(HD+VDRSA)}	4	77.01	3.22	0.037	8.03
{S(SDI+MAT)}	4	77.12	3.33	0.035	8.14
{S(HD+MAT)}	4	77.16	3.37	0.034	8.18
{S(LSA+MAT)}	4	77.24	3.45	0.033	8.26
{S(HD+VDRSA+SDI)}	5	78.73	4.94	0.016	9.75
{S(HD+VDRPER+HD*VDRPER)}	5	78.88	5.09	0.014	9.90
{S(HD+VDRSA+HD*VDRSA)}	5	79.08	5.29	0.013	10.10
{S(LSA+MAT+LSA*MAT)}	5	79.10	5.31	0.013	10.12
{S(HD+MAT+HD*MAT)}	5	79.17	5.38	0.013	10.19

The exploratory addition of lake surface area (LSA) to the landscape interaction model S(LSA + FL10 + BP10 + FL10*BP10) significantly improved the initial model and ranked second in the all models suite (Table 24). The effects of landscape covariates and their interactions were similar to the most parsimonious model; however, there was a moderately strong negative effect of lake surface area on chick survival ($\beta = -0.748$, 95% CI = -1.705-0.210).

An exploratory model allowing survival rate to vary during each of the 4 time intervals [i.e., model = $S((4age)FL10+BP10+FL10*BP10)$] did not improve model fit (QAICc=72.682, $\Delta QAICc=8.843$) (Table 23).

Table 23. Exploratory suite chick survival model results.

Model	k	QAICc	$\Delta QAICc$	Wi
<u>Exploratory suite</u>				
{S(MAT+FL10+BP10+FL10*BP10)}	6	63.84	0.00	0.848
{S(LSA +FL10+BP10+FL10*BP10)}	6	68.85	5.01	0.069
{S(MAT+FL10+BP10)}	5	69.49	5.65	0.050
{S(VDRSA+FL10+BP10+FL10*BP10)}	6	71.06	7.22	0.023
{S(4ages)FL10+BP10+FL10*BP10)}	7	72.68	8.84	0.010

Table 24. Combined suite chick survival model results depicting models containing 0.95 of model weight.

Model	k	QAICc	$\Delta QAICc$	Wi
{S(MAT+FL10+BP10+FL10*BP10)}	6	63.84	0.00	0.737
{S(LSA +FL10+BP10+FL10*BP10)}	6	68.85	5.01	0.060
{S(FL10+BP10+FL10*BP10)}	5	68.98	5.14	0.056
{S(MAT+FL10+BP10)}	5	69.49	5.65	0.044
{S(VDRSA+FL10+BP10+FL10*BP10)}	6	71.06	7.22	0.020
{S(4ages)FL10+BP10+FL10*BP10)}	7	72.68	8.84	0.009
{S(FL10)}	3	72.72	8.88	0.009
{S(HD+VDRSA+HD*VDRSA)}	2	72.86	9.02	0.008
{S(FL10+BP10)}	4	72.96	9.12	0.008

I used model averaging to obtain estimates of covariates for models where a model weight was 0.001 or greater. Exploratory models were included in the model averaging procedure. Model averaged beta effects were similar to beta effects from best approximating models (Tables 25 and 26). The 95% confidence intervals on model averaged beta estimates often overlapped zero. These estimates should be viewed as conservative effects of each individual covariate on chick DSR.

Table 25. Model averaged chick survival parameter estimates.

Covariate	Beta Estimate	95% CI	
INTERCEPT	2.073	-0.271	4.418
AGE	1.767	-3.159	6.693
AGE2	-2.088	-4.000	-0.176
AGE3	-0.597	-2.771	1.576
AGE4	0.467	-1.936	2.870
BP10	0.466	-0.730	1.663
FL10	1.882	-0.009	3.773
FL10*BP10	-0.388	-1.234	0.458
HD	0.014	-0.335	0.363
LSA	-0.712	-2.100	0.676
MAT	-0.084	-1.079	0.911
SDI	-0.724	-2.411	0.963
VDRPER	-0.426	-2.007	1.154
VDRSA	0.287	-1.707	2.281
YEAR	0.485	-1.481	2.450

Table 26. Beta estimates from 5 highest ranking Chick Survival Models.

Model and Model Structure	K	B Estimate	95% CI	
<hr/>				
S = MAT + FL10 + BP10 + FL10*BP10				
<hr/>				
S = $\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{MAT}) + \beta_3(\text{FL10}) + \beta_4(\text{BP10}) + \beta_5(\text{FL10*BP10})$	6	$\beta_0 = 1.86$	-0.682	4.411
		$\beta_1 = 1.71$	0.322	3.096
		$\beta_2 = -0.09$	-0.145	-0.025
		$\beta_3 = 1.99$	0.312	3.661
		$\beta_4 = 0.50$	-0.167	1.159
		$\beta_5 = -0.38$	-0.725	-0.031
<hr/>				
S = LSA + FL10 + BP10 + FL10*BP10				
<hr/>				
S = $\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{LSA}) + \beta_3(\text{FL10}) + \beta_4(\text{BP10}) + \beta_5(\text{FL10*BP10})$	6	$\beta_0 = 1.34$	-1.397	4.072
		$\beta_1 = 1.92$	0.582	3.255
		$\beta_2 = -0.75$	-1.705	0.210
		$\beta_3 = 2.38$	0.228	4.524
		$\beta_4 = 0.73$	-0.072	1.533
		$\beta_5 = -0.53$	-0.995	-0.058
<hr/>				
S = FL10 + BP10 + FL10*BP10				
<hr/>				
S = $\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{FL10}) + \beta_3(\text{BP10}) + \beta_4(\text{FL10*BP10})$	5	$\beta_0 = 1.68$	-0.912	4.281
		$\beta_1 = 2.01$	0.692	3.326
		$\beta_2 = 1.69$	-0.102	3.481
		$\beta_3 = 0.50$	-0.180	1.182
		$\beta_4 = -0.38$	0.773	0.015
<hr/>				
S = MAT + FL10 + BP10				
<hr/>				
S = $\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{MAT}) + \beta_3(\text{FL10}) + \beta_4(\text{BP10})$	5	$\beta_0 = 3.92$	2.667	5.582
		$\beta_1 = 1.92$	0.591	3.253
		$\beta_2 = -0.06$	-0.109	-0.010
		$\beta_3 = 0.46$	0.082	0.840
		$\beta_4 = -0.23$	-0.511	0.047
<hr/>				
S = VDRSA + FL10 + BP10 + FL10*BP10				
<hr/>				
S = $\beta_0 + \beta_1(\text{AGE}) + \beta_2(\text{VDRSA}) + \beta_3(\text{FL10}) + \beta_4(\text{BP10}) + \beta_5(\text{FL10*BP10})$	6	$\beta_0 = 1.83$	-1.114	4.767
		$\beta_1 = 2.01$	0.690	3.324
		$\beta_2 = -0.56$	-5.997	4.885
		$\beta_3 = 1.67$	-0.101	3.450
		$\beta_4 = 0.49$	-0.190	1.175
		$\beta_5 = -0.38$	-0.769	0.013

The predicted negative effects of human development and recreation received moderate support when disturbance suite models were combined with all other models (Table 24, Appendix A). Single predictor models containing covariates of human use received little support (i.e., S(MAT), $\Delta \text{QAICc} = 11.363$, S(VDRSA), $\Delta \text{QAICc} = 11.347$, and S(VDRPER), $\Delta \text{QAICc} = 11.075$). Models incorporating human use covariates with landscape covariates received strong support, and significantly improved the landscape interaction model (Table 23, Table 24). The model: S(MAT + FL10 + BP10 + FL10*BP10, with a $\text{QAICc} = 63.839$, and $\Delta \text{QAICc} = 0.00$ ranked first in the all models suite. The second most parsimonious model was created with the exploratory addition of lake surface area (LSA) to the landscape interaction model. S(LSA + FL10 + BP10 + FL10*BP10) ($\text{QAICc} = 68.850$, $\Delta \text{QAICc} = 5.011$) (Table 24).

The most parsimonious model showed a strong positive effect of age on survival ($\beta = 1.709$, 95% CI = 0.322-3.096). There was a strong negative effect of mean angler trips (MAT) on chick survival ($\beta = -0.085$, 95% CI = -0.145- -0.025). Survival increased as the number of feeding lakes and the number of breeding pairs increased within a 10 km radius of the hatch lake. An increase in feeding lakes produced the greatest positive effect on survival ($\beta = 1.986$, 95% CI = 0.312- 3.66) followed by breeding pairs ($\beta = 0.496$, 95% CI = -0.167 -1.159). The landscape interaction term (FL10*BP10) yielded a strong negative effect on chick survival ($\beta = -0.378$, 95% CI = -0.725- -0.031) (Figure 2, Table 26).

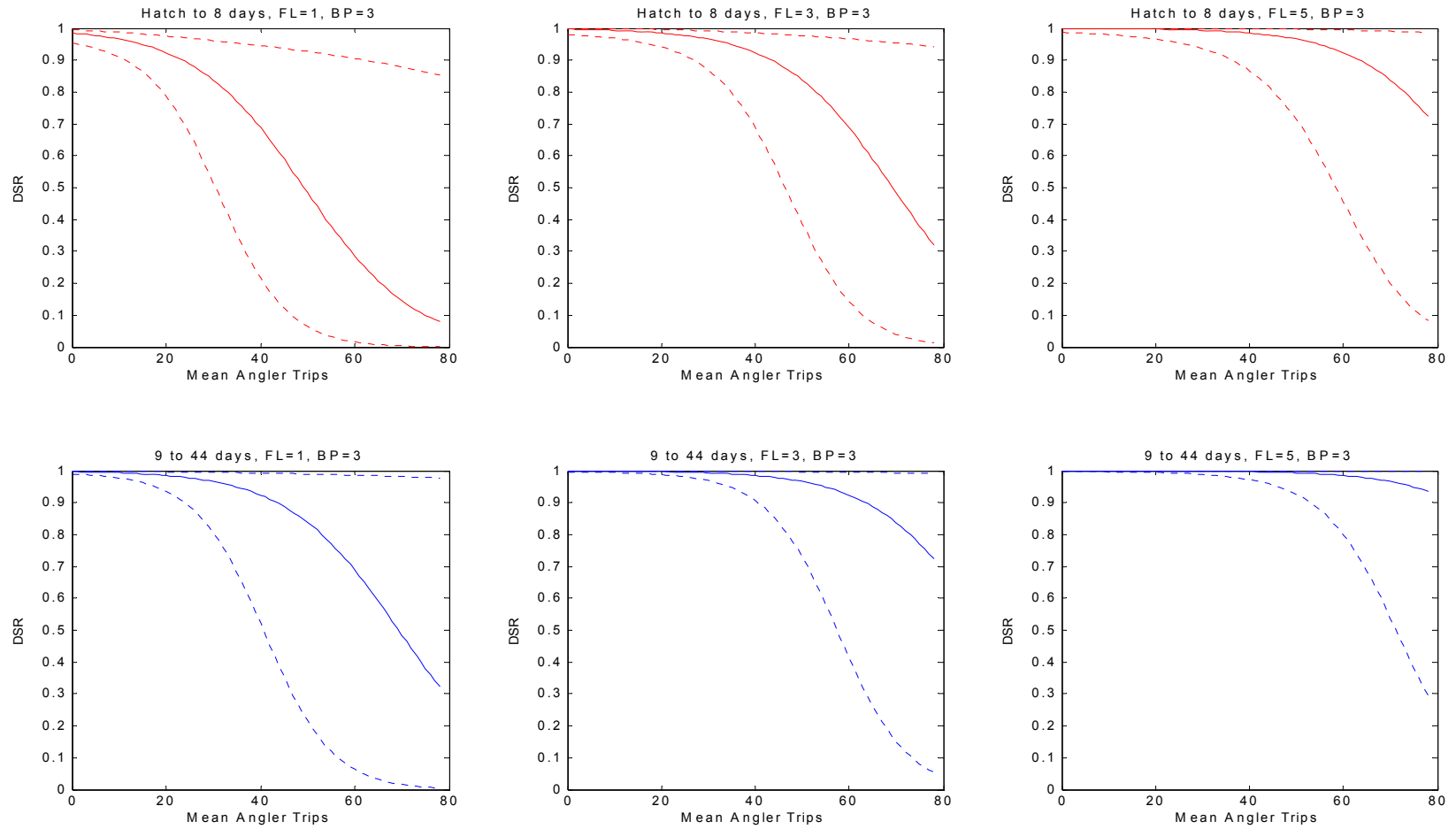


Figure 2. Common Loon chick daily survival, top three panels depict daily survival during the first 8 days after hatching as the number of foraging lakes within 10 km increases from one to five, bottom three panels depict chick daily survival from 9-44 days as the number of foraging lakes within 10 km increases from one to five.

DISCUSSION

The model results demonstrated complex relationships between multi-scaled covariates and the survival rate of Common Loon chicks in Northwest Montana. Fifty of the 65 chicks hatched (77%) survived the 44-day observation period. A 77% chick survival rate is comparable to other studies of chick survival, and is only slightly higher than the average 75% chick survival rate of all studies combined (Table 27). Kelly (1992) reported a 90% survival rate for loon chicks monitored on many of the same Montana lakes as this study (Table 27).

Table 27. Survival rate of common loon chicks from various study sites.

Chick Survival Rate	Chicks Hatched	Chicks Survived	Location	Source
53%	40	21	Maine	Christenson 1981
68%	31	21	Minnesota	Olson and Marshall 1952
94%	36	34	Minnesota	McIntyre 1975
68%	117	79	Saskatchewan	Yonge 1981
90%	87	78	Montana	Kelly 1992
77%	65	50	Montana	Present Study
(Totals) 75%	376	283	All	All

During the study, only 3 chicks were hatched on PLT territories and all were on the same lake. This was not sufficient to reliably estimate chick survival rates on PLT territory lakes. Consequently, I combined the three chicks from PLT territories with the chicks from WLT territories. Predictably, this resulted in extreme correlation between the new two category territory covariate and lake surface area, since the new territory covariate was essentially only a cutoff of lakes smaller than 60 acres and lakes larger than

60 acres. As a result of correlations with lake surface area (LSA) and other covariates, I decided to remove the territory covariate from the chick survival analysis and use lake surface area (LSA). This limited my ability to draw inference about density dependent affects on chick survival, however, it still allowed me to analyze differences in survival rates of chicks on large lakes that supply all needed forage resources for adults and small lakes, where adults sometimes fly to and defend nearby lakes as forage areas.

I observed strong landscape scale effects on chick survival rates. The two best approximating models across all suites included a single lake scale predictor with multiple landscape scale predictors. I propose two explanations for the positive effect of feeding lakes within a 10-km radius of the nesting lake. First, relevant to loon broods reared on small lakes (i.e., <60 acres) where adults utilize adjacent lakes for foraging (MLT, Evers 2001), more foraging lakes near the nesting lake may offer several advantages: first, a high number of nearby foraging lakes provides loons multiple opportunities to maximize foraging efficiency under the given conditions. A loon could select the lake with a minimum of surface area disturbance from boat traffic and the highest density of forage fish. These two factors may combine to minimize the length of time an adult spends away from its chicks and expose them to higher predation. During this study I never observed chicks unattended by at least one adult; however, on the smallest lakes I occasionally observed a single adult tending to the brood while the other adult was not present on the lake. Second, a positive effect of nearby foraging lakes on chick survival may derive from reduction in the number of territorial conflicts between chick rearing adults and non-breeding “floater” individuals or pairs. A high number of

available forage lakes may give non-territorial birds a place to forage without intruding into a breeding territory. Conflicts can separate chicks from adults for extended periods of time making them vulnerable to predation or exposure.

My analysis also indicated a weak positive effect of the number of breeding pairs near the nesting lake on chick survival. A high number of breeding pairs within a 10-km radius could indicate overall habitat quality within the landscape. When numerous nesting pairs exist within a 10-km radius of a lake, this could indicate the presence of a cluster of lakes suitable for nesting and foraging. Mean angler trips (MAT) was a stronger predictor of chick survival than other forms of disturbance. This supports a hypothesis that larger lake areas or perimeters may not mitigate the effects of disturbance as much as previously thought by some researchers (Strong and Bissonette 1989, Vermeer 1973).

The results of the AIC analysis supported three of my five lake scale hypotheses: a negative effect of disturbance and lake surface area, and a weak positive effect of increasing yellow perch density. The negative effect of lake surface supports a hypothesis offered by Yonge (1981), who speculated that McIntyre (1975) saw very high chick survival (94%) because most lakes in her study area were small eutrophic lakes with abundant food and isolated loon pairs. Olson and Marshal (1952) saw much lower survival (68%) on study lakes that were large, unproductive waters inhabited by numerous loons. Davis (1972) found starvation was the main factor contributing to chick mortality in Arctic (*Gavia arctica*) and Red-throated (*Gavia stellata*) Loons. Since energy demands of chicks are highest immediately following hatch (McIntyre 1975),

chicks on small lakes may benefit energetically during the initial weeks of life on MLT lakes in my study area.

While there was a positive effect of high densities of yellow perch ($\beta=3.29$, 95% CI = 2.419-4.163) the model was not well supported in the AIC analysis (S(YP) (Δ QAICc=10.761). The AIC analysis did not support the hypothesized positive effect of shoreline development index. I also found no support for the hypothesized negative effect of mean lake depth (MLD). My exploratory investigation of the effect of age on survival supports other research (Olson 1951, Yonge 1981) indicating that most chick mortality occurred during the first week post-hatch. After the first week, survival increased dramatically and remained high until fledging.

Management Implications

The results of my analysis using AIC methods emphasized the need for managers to consider not only lake scale habitat conditions but also landscape level habitat factors. Efforts to increase chick survival should focus on minimizing the negative effects of human recreation, especially during the first week after hatching. Temporary “no wake” restrictions or using floating signs to eliminate watercraft use in historical chick nursery areas may be necessary to protect nesting loons and chicks. Minimizing surface area disturbances on potential forage lakes surrounding smaller nesting lakes should also be a priority, because it may maximize foraging efficiency and reduce the number of lakes needed to support loons nesting on small lakes. Many small lakes are privately owned or currently have limited access. This means efficient

communications with landowners regarding wise land use options around private lakes is essential.

My results highlight the need for continued research from a lake and landscape scale perspective. More detailed investigations about chick survival in relation to loon density and carrying capacities of the landscape may help to pinpoint critical lakes of high conservation priority. Continued research concerning forage lake characteristics surrounding small nesting lakes is needed to guide forage lake protection efforts and to maintain the future loon productivity of these small but valuable lakes.

CONCLUSIONS

The results demonstrated complex relationships between the independent variables I observed and daily survival rate of common loon nests and chicks in Northwest Montana. I found a strong effect of territory type, lake perimeter, and the shoreline development index on daily nest survival (Table 11). Loon nests located on small lakes (<60 acres) had the highest DSR followed closely by nests on large lakes (>60 acres) with one nesting pair. Large lakes with two or more nesting pairs produced significantly lower DSR. Lake perimeter and shoreline development (SDI) were highly correlated, and the top ranked models indicated that DSR increased as perimeter, or the shoreline development increased in any territory type. I hypothesize that increased perimeter or shoreline development indices provide loons with greater nest site options, and furthermore, I speculate that an increase in shoreline habitat complexity may increase time required for a predator to detect and exploit loon nest sites.

Lakes within my study area encompassed a large gradient of recreation and lakeshore development. Surprisingly, my modeling results did not directly support a strong effect of human recreation or development on nest DSR. However, the data do provide indirect evidence that development and recreation may be reducing nest DSR. For example, when I examined mean covariate values by territory type (Table 14) PLT's which experienced the lowest nest DSR, had the highest measures of all three disturbance covariates. In particular MAT which ranged from 1.38 angler trips on MLT territories to 55.57 angler trips on PLT territories. Disturbance suite models also suggested that

among the three forms of disturbance measured, MAT was having the strongest affect on nest DSR.

Chick survival was most parsimoniously estimated by landscape scale habitat features and lake scale disturbance effects. Fifty of the 65 chicks hatched (77%) survived the 44 day observation period. The 77% survival rate I detected is comparable to other studies of chick survival, and is only slightly higher than the total average (75%) chick survival rate pooled across all studies (Table 27). Chick mortality was highest during the first 8 days after hatching, and decreased dramatically over the remainder of the monitoring period. My data supported a negative effect of recreation on chick DSR. I observed a positive effect of the number of foraging lakes within 10 km of the nesting lake on chick survival. Survival rates remained high over an increasing level of recreation use as the number of nearby foraging lakes increased. This could indicate human recreation on chick rearing lakes in Montana reduced adult foraging efficiency, and ultimately lead to reduced amounts of food fed to chicks and lower attentiveness to broods. Adult loons may have offset this forage reduction by utilizing nearby lakes where they fed quickly and efficiently, allowing them to devote more effort to feeding and protecting chicks.

The results of my research may alert managers to consider not only lake scale habitat conditions, but also landscape level habitat factors, including the distribution and quality of multi-lake settings in a landscape framework. The traditional approach of focusing management toward single lakes and ignoring complex multi-lake territories was not supported. Although classifying lakes by territory type appeared to be relevant

to management, future efforts need to focus not only on lake type, but on preserving shoreline nesting habitat and minimizing shoreline and surface area disturbance, especially on highly productive MLT lakes. The extensive nest signing and public education efforts currently being conducted by Montana FWP and the Montana Loon Society may be effectively mitigating some of the hypothesized negative effects of recreation and development on nest DSR. However, disturbance suite models that I assessed suggested MAT was having an impact on nest DSR. Consequently, future education efforts should be directed at anglers and other watercraft users, especially on PLT lakes where disturbance factors were highest (Table 28).

Table 28. Nest Survival management prescriptions and priority based on nesting territory type.

Territory	Management Prescription	Management Priority
MLT	<ol style="list-style-type: none"> 1. Work with landowners to preserve and improve existing nesting habitat. 2. Reduce effects of watercraft recreation through "no wake" restrictions. Encourage use of smaller non-motorized watercraft through fewer improved access points. 3. Identify potential nearby forage lakes, minimize recreation disturbance on these lakes to maximize foraging efficiency. 	High
WLT	<ol style="list-style-type: none"> 1. Preserve existing nesting habitat. 2. Reduce disturbance through "no wake" restrictions near shorelines and islands, while leaving large areas away from shorelines available for recreation. 	Moderate
PLT	<ol style="list-style-type: none"> 1. Preserve existing nesting habitat. 2. Reduce disturbance through "no wake" restrictions near shorelines and islands, while leaving large areas away from shorelines available for recreation. 3. Conduct extensive public education efforts using Loon Rangers targeted at anglers and other watercraft users to reduce boat activity near nest sites. 4. Deploy floating signs to reduce boat activity near nest sites. 	Moderate

Efforts to minimize the negative effects of angling recreation especially during the first week post hatch may provide the largest benefit to chick survival in the study area. Minimizing surface area disturbances on potential forage lakes surrounding smaller nesting lakes should also be a priority (Table 29).

Table 29 . Loon chick survival management prescriptions and priorities based on habitat conditions of chick rearing lake.

Habitat conditions of lake with chicks		Management Prescription	Management Priority
Surface Area	Forage Lakes		
Surface Area < 60 acres	0-2 foraging lakes within 10 km radius	1. Reduce watercraft disturbance through "no wake" restrictions on entire lake. 2. Minimize watercraft disturbance on nearby potential forage lakes. 3. Encourage non-motorized watercraft use, leave access points in primitive condition. 4. Extensive public education using Loon Rangers. Encourage responsible watercraft use near loon broods.	Very High
	3 or more foraging lakes within 10 km radius	1. Extensive public education using Loon Rangers. Encourage responsible watercraft use near loon broods.	Moderate
Surface Area > 60 acres	0-2 foraging lakes within 10 km radius	1. Reduce watercraft disturbance through "no wake" restrictions along shorelines. 2. Extensive public education using Loon Rangers. Encourage responsible watercraft use near loon broods. 3. Use floating signs around frequently used chick rearing habitat to reduce boat use in these habitats.	High
	3 or more foraging lakes within 10 km radius	1. Extensive public education using Loon Rangers. Encourage responsible watercraft use near loon broods.	Moderate

More research is needed to test hypotheses generated by this project.

Validation of the predictive power of the models generated through this research is necessary. Models should be tested over multiple field seasons in the study area where the data were collected as well as in the Blackfoot/Clearwater lake complex not included in this study. These results highlight the need for continued research from a lake and landscape scale perspective. More detailed investigations about nest and chick DSR in relation to loon density and carrying capacities of the landscape may help to pinpoint critical lakes of high conservation priority. Common loons in northwest Montana may be near the region's carrying capacity given current habitat condition and the presence of apparently surplus floating individuals in the population. Research about forage lake characteristics surrounding small nesting lakes is needed to guide forage lake protection efforts to maintain the future loon productivity of these small but valuable lakes. Finally, telemetry could be employed to investigate the frequency of multiple lake use by adults on different lake types during nesting and chick rearing.

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APPENDICES

APPENDIX A

COMMON LOON NEST DSR AND CHICK SURVIVAL MODEL OUTPUT
FROM ALL MODELS SUITE

Combined suite common loon nest DSR model results.

Model	k	AICc	Δ AICc	Wi
{DSR(TER + PERIM)}	4	191.98	0.00	0.271
{DSR(TER + SDI)}	4	192.98	1.01	0.164
{DSR(TER + PERIM + TER*PERIM)}	6	194.29	2.31	0.085
{DSR(TER + FL10 + TER*FL10)}	6	194.69	2.71	0.070
{DSR(TER + LSA)}	4	195.11	3.13	0.057
{DSR(TER + VDRPER + TER*VDRPER)}	3	195.16	3.18	0.055
{DSR(TER + VDRSA)}	4	195.91	3.93	0.038
{DSR(TER + BP10)}	4	195.93	3.95	0.038
{DSR(TER + SDI + TER*SDI)}	6	195.96	3.98	0.037
{DSR(TER)}	3	196.03	4.05	0.036
{DSR(TER + MAT + TER*MAT)}	5	196.38	4.40	0.030
{DSR(TER + BP10 + TER*BP10)}	6	196.87	4.89	0.023
{DSR(TER + VDRPER)}	4	197.24	5.26	0.020
{DSR(TER + FL10)}	4	197.75	5.77	0.015
{DSR(TER + MAT)}	4	198.04	6.06	0.013
{DSR(TER + FL10 + BP10 + FL10*BP10)}	6	198.18	6.20	0.012
{DSR(GLOBAL)}	18	198.28	6.30	0.012
{DSR(TER + VDRSA + TER*VDRSA)}	6	198.44	6.46	0.011
{DSR(TER + LSA + TER*LSA)}	6	198.49	6.51	0.010
{DSR(SDI + MAT + SDI*MAT)}	4	201.37	9.39	0.002
{DSR(MAT + NCOV + MAT*NCOV)}	8	204.95	12.97	0.000
{DSR(BPLAKE)}	2	207.27	15.29	0.000
{DSR(VDRPER + NCOV + WD1M)}	5	207.32	15.35	0.000
{DSR(MAT)}	2	209.24	17.26	0.000
{DSR(WD1M + MAT)}	3	209.48	17.50	0.000
{DSR(VDRPER + NCOV)}	5	210.06	18.08	0.000
{DSR(MAT + NCOV)}	5	210.43	18.45	0.000
{DSR(MAT + NCOV + NL)}	7	210.78	18.80	0.000
{DSR(LSA + MAT)}	3	211.01	19.03	0.000
{DSR(SDI + MAT)}	3	211.23	19.26	0.000
{DSR(MAT + LSA + WD1M)}	4	211.34	19.36	0.000
{DSR(VDRPER)}	2	211.47	19.49	0.000
{DSR(MAT + NCOV + LSA)}	6	212.03	20.05	0.000
{DSR(WD1M + NL)}	4	212.07	20.09	0.000
{DSR(MAT + SDI + NCOV)}	6	212.44	20.46	0.000
{DSR(LSA + MAT + LSA*MAT)}	4	212.64	20.66	0.000
{DSR(VDRPER + NCOV + VDRPER*NCOV)}	8	213.11	21.13	0.000
{DSR(VDRSA + NCOV + VDRSA*NCOV)}	8	214.18	22.20	0.000
{DSR(NL + PERIM + NL*PERIM)}	6	214.44	22.46	0.000
{DSR(PERIM)}	2	214.76	22.78	0.000
{DSR(NCOV + NL + WD1M)}	7	214.87	22.89	0.000
{DSR(VDRSA + NCOV + WD1M)}	6	215.51	23.53	0.000
{DSR(LSA)}	2	216.06	24.08	0.000
{DSR(VDRSA)}	2	216.27	24.29	0.000
{DSR(.)}	1	216.49	24.51	0.000

Combined suite common loon nest DSR model results cont.

Model	k	AICc	Δ AICc	Wi
{DSR(NL + PERIM)}	4	216.54	24.56	0.000
{DSR(LSA + MLD + SDI)}	4	216.69	24.71	0.000
{DSR(SDI + PERIM)}	3	216.69	24.71	0.000
{DSR(VDRSA + NCOV)}	5	217.09	25.11	0.000
{DSR(NL + NCOV + NL*NCOV)}	9	217.35	25.38	0.000
{DSR(YEAR)}	2	217.40	25.42	0.000
{DSR(WTRFL)}	2	217.49	25.51	0.000
{DSR(SDI)}	2	217.52	25.54	0.000
{DSR(BP10)}	2	217.62	25.64	0.000
{DSR(MLD)}	2	218.40	26.42	0.000
{DSR(VDRSA + NL + NCOV)}	7	218.41	26.43	0.000
{DSR(FL10)}	2	218.44	26.46	0.000
{DSR(NCOV)}	4	219.34	27.36	0.000
{DSR(NL)}	3	219.45	27.47	0.000
{DSR(SDI + NL)}	4	219.58	27.60	0.000
{DSR(VDRSA + NL + NCOV + YEAR)}	8	219.65	27.67	0.000
{DSR(WTRFL + NL)}	4	220.00	28.02	0.000
{DSR(SDI + NL + SDI*NL)}	6	220.37	28.39	0.000
{DSR(NL + NCOV)}	6	222.50	30.52	0.000
{DSR(WTRFL + NL + WTRFL*NL)}	6	223.44	31.46	0.000
{DSR(NL + NCOV + YEAR)}	7	224.00	32.02	0.000

Combined suite chick survival model results.

Model	K	QAICc	Δ QAICc	Wi
{S(MAT+FL10+BP10+FL10*BP10)}	6	63.84	0.00	0.737
{S(LSA +FL10+BP10+FL10*BP10)}	6	68.85	5.01	0.060
{S(FL10+BP10+FL10*BP10)}	5	68.98	5.14	0.056
{S(MAT+FL10+BP10)}	5	69.49	5.65	0.044
{S(VDRSA+FL10+BP10+FL10*BP10)}	6	71.06	7.22	0.020
{S(4ages)FL10+BP10+FL10*BP10)}	7	72.68	8.84	0.009
{S(FL10)}	3	72.72	8.88	0.009
{S(HD+VDRSA+HD*VDRSA)}	2	72.86	9.02	0.008
{S(FL10+BP10)}	4	72.96	9.12	0.008
{S(BP10)}	3	72.98	9.15	0.008
{S(SDI+MAT+SDI*MAT)}	5	73.79	9.95	0.005
{S(YP)}	4	74.60	10.76	0.003
{S(VDRPER)}	3	74.91	11.07	0.003
{S(ATSA)}	3	75.06	11.22	0.003
{S(SDI)}	3	75.09	11.26	0.003
{S(HD)}	3	75.14	11.30	0.003
{S(VDRSA)}	3	75.19	11.35	0.003
{S(MAT)}	3	75.20	11.36	0.003
{S(YEAR)}	3	75.22	11.38	0.002
{S(LSA)}	3	75.28	11.44	0.002
{S(TIME)}	4	76.83	12.99	0.001
{S(HD+VDRPER)}	4	76.85	13.01	0.001
{S(SDI+MLD)}	4	76.99	13.15	0.001
{S(HD+VDRSA)}	4	77.01	13.17	0.001
{S(HD+MAT+HD*MAT)}	4	77.08	13.24	0.001
{S(SDI+MAT)}	4	77.12	13.28	0.001
{S(HD+MAT)}	4	77.16	13.32	0.001
{S(HD+YEAR)}	4	77.17	13.33	0.001
{S(PIKE+VDRSA)}	4	77.21	13.37	0.001
{S(LSA+MAT)}	4	77.24	13.41	0.001
{S(HD+YEAR+HD*YEAR)}	5	78.10	14.27	0.001
{S(PIKE+VDRSA+PIKE*VDRSA)}	5	78.56	14.72	0.000
{S(SDI+MLD+YP)}	6	78.70	14.86	0.000
{S(HD+VDRSA+SDI)}	5	78.73	14.89	0.000
{S(HD+VDRPER+HD*VDRPER)}	5	78.88	15.04	0.000
{S(SDI+MLD+SDI*MLD)}	5	79.01	15.17	0.000
{S(LSA+MAT+LSA*MAT)}	5	79.10	15.26	0.000
{S(.)}	1	82.75	18.91	0.000
{S(GLOBAL*)}	16	84.89	21.05	0.000
{S(HD+HD^2)}	4	32390.01	32326.17	0.000

APPENDIX B

HABITAT CONDITIONS OF LAKES SUPPORTING COMMON LOON NESTS AND
CHICK BROODS IN NORTHWEST MONTANA 2004, 2005

Summary of DSR habitat and disturbance covariates on lakes with Common Loon nests in Northwest Montana 2004, 2005.

Lake Name	LSA (km ²)	Perim (km)	SDI	MLD	VDRSA	VDRPER	MAT	BP10	FL10	TER	BPLAKE
Rogers	0.97	4.34	1.25	2.72	0.230	0.0127	36.0	2	2	WLT	1
Lone	0.54	3.51	1.35	9.14	0.038	0.0014	1.0	6	3	WLT	1
Monroe	0.19	2.59	1.66	4.57	0.000	0.0000	0.0	6	2	MLT	1
Ashley	11.53	26.55	2.21	27.12	0.108	0.0116	84.0	5	2	PLT	4
Upper Thompson (middle)	0.34	2.99	1.46	6.41	0.482	0.0134	74.5	1	8	PLT	2
Upper Thompson (east)	0.42	3.39	1.48	6.41	0.337	0.0103	74.5	1	7	PLT	2
Island	0.85	6.40	1.95	6.04	0.166	0.0055	2.0	0	1	WLT	1
Blanchard	0.60	5.95	2.18	3.96	0.211	0.0052	41.5	1	11	WLT	1
Boyle	0.16	1.90	1.35	2.44	0.000	0.0000	0.0	3	8	MLT	1
Tally	4.90	13.47	1.72	72.85	0.008	0.0007	18.5	2	5	WLT	1
Bootjack	0.14	2.49	1.87	5.55	0.229	0.0032	16.5	4	12	MLT	1
Lower Stillwater	1.01	7.35	2.06	4.18	0.144	0.0049	23.5	7	3	WLT	1
Upper Stillwater	2.40	18.09	3.30	6.13	0.025	0.0008	5.5	4	6	PLT	3
Dog	0.41	4.33	1.91	3.05	0.099	0.0023	4.5	4	6	WLT	1
Winona	0.19	1.87	1.21	3.05	0.000	0.0000	0.0	2	2	MLT	1
Garnet/Mud	0.06	1.24	1.47	1.20	0.214	0.0024	0.0	1	1	MLT	1
Spoon	0.24	2.33	1.35	3.20	0.559	0.0141	5.0	1	1	WLT	1
Cedar Creek Res.	0.13	2.29	1.79	2.40	0.000	0.0000	0.0	1	4	MLT	1
Tepee	0.17	1.83	1.24	1.52	0.116	0.0027	0.0	1	1	MLT	1
Dickey	2.37	7.79	1.43	13.66	0.067	0.0050	8.5	4	2	WLT	1
Murphy	0.57	3.28	1.23	3.26	0.071	0.0030	8.5	4	4	WLT	1
Martin	0.14	1.83	1.37	2.13	0.143	0.0027	0.0	4	3	MLT	1
Bull (Stryker)	0.43	5.84	2.52	11.58	0.198	0.0036	8.5	7	2	WLT	1
Gayle's Pond	0.02	0.69	1.37	3.66	0.200	0.0014	0.0	7	2	MLT	1
Frank	0.60	6.71	2.44	6.10	0.664	0.0148	79.0	3	11	WLT	1
Marl	0.44	2.94	1.26	12.31	0.028	0.0010	13.5	5	7	WLT	1
Lick	0.08	1.17	1.19	2.01	0.053	0.0009	0.0	1	10	MLT	1
Loon (Trego)	0.15	2.37	1.75	3.20	0.028	0.0004	0.0	5	4	MLT	1

Chick survival covariate values collected on lakes with common loon chicks in Northwest Montana 2004, 2005.

Lake Name	LSA (km ²)	SDI	MLD (m)	VDRSA	VDRPER	Pike	Yellow Perch	MAT	AT/SA	BP10	FL10
Rogers	0.97	1.25	2.72	0.230	0.0127	No	None	35	36.2	2	2
Lone	0.54	1.35	9.14	0.038	0.0014	Yes	Abundant	2	3.7	6	3
Monroe	0.19	1.66	4.57	0.000	0.0000	Yes	Abundant	1	5.2	6	2
Island	0.85	1.96	6.04	0.108	0.0055	No	Abundant	4	4.7	0	1
Blanchard	0.60	2.18	3.96	0.211	0.0052	Yes	Abundant	52	87.4	1	11
Boyle	0.16	1.35	2.44	0.000	0.0000	Yes	None	0	0.0	3	8
Tally	4.90	1.72	72.85	0.008	0.0007	Yes	None	24	4.9	2	5
Bootjack	0.14	1.87	5.55	0.229	0.0032	No	None	14	98.6	4	12
Lower Stillwater	1.01	2.06	4.18	0.144	0.0049	Yes	Abundant	28	27.7	7	3
Upper Stillwater	2.40	3.30	6.13	0.025	0.0008	Yes	Abundant	4	1.7	4	6
Dog	0.41	1.91	3.05	0.099	0.0023	Yes	Abundant	8	19.6	4	6
Garnet/Mud	0.06	1.47	1.20	0.214	0.0024	No	None	0	0.0	1	1
Spoon	0.24	1.35	3.20	0.560	0.0141	No	None	0	0.0	1	1
Cedar Creek Res.	0.13	1.79	2.40	0.000	0.0000	No	None	0	0.0	1	4
Tepee	0.17	1.52	1.52	0.116	0.0027	No	None	0	0.0	1	1
Dickey	2.37	1.43	13.66	0.067	0.0050	No	None	8	3.4	4	2
Murphy	0.57	1.23	3.26	0.071	0.0030	Yes	Rare	10	17.5	4	4
Martin	0.14	2.13	2.13	0.143	0.0027	Yes	None	0	0.0	4	3
Bull (Stryker)	0.43	2.52	11.58	0.198	0.0036	No	None	6	14.0	7	2
Gayle's Pond	0.02	1.37	3.66	0.200	0.0014	No	None	0	0.0	7	2
Frank	0.60	2.44	6.10	0.664	0.0148	No	None	78	129.4	3	11
Marl	0.44	1.26	12.31	0.028	0.0010	Yes	Abundant	25	57.2	5	7
Lick	0.08	1.20	2.01	0.053	0.0009	No	None	0	0.0	1	10